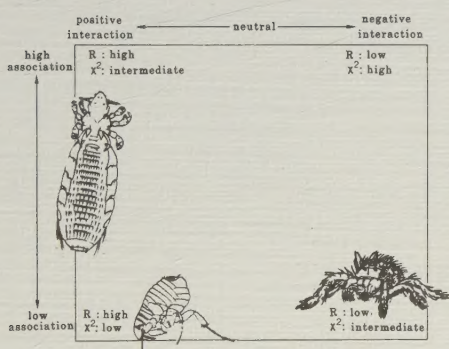


Life tactics and distribution of small mammal ectoparasites (Anoplura, Siphonaptera and Acari) in northernmost Fennoscandia

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LIFE TACTICS AND DISTRIBUTION OF SMALL MAMMAL ECTOPARASITES

(ANOPLURA, SIPHONAPTERA AND ACARI)

IN NORTHERNMOST FENNOSCANDIA

LARS LUNDQVIST

Fk, Hb

Akademisk avhandling, som för avläggande av filosofie doktorsexamen vid matematisk-naturvetenskapliga fakulteten vid Lunds universitet kommer att offentligens försvaras å Ekologihusets föreläsningssal, Helgonavägen 5, Lund, fredagen den 10 maj 1985, kl 0900.

Dedicated to my parents
and to Mårten and Oskar;
my roots and anchors.

LIFE STRATEGIES AND DISTRIBUTION OF SMALL MAMMAL ECTOPARASITES

(ANOPLURA, SIPHONAPTERA AND ACARI)

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DISSERTATION

Lund 1985

Abstract

Among ectoparasites (Insecta: Anoplura, Siphonaptera, Acari: Laelapidae, Ixodidae), life tactics may from an evolutionary aspect be coupled to either full-time or part-time parasitism. The dichotomy is based on whether the parasites stay on one host individual during their life time or forage on a number of hosts. When staying on one host, the parasites have a continuous access to food, but risk to die with the host. Therefore, they have shortened their generation-time and are iteroparous. By repeated host changes, the parasites minimize the risk of being killed by or with the host. On the other hand, there is a danger of not finding a new host. Part-time ectoparasites can increase their success by using several host species and increasing their ability to wait. This prolongs the generation time and leads to semelparity. Deductive predictions from the model are tested on a material of small mammal hosts and ectoparasites from northernmost Fennoscandia.

Ectoparasite has a broad meaning, and external parasites have been reported among numerous insect orders, e.g. Dermaptera, Diptera, Lepidoptera and Coleoptera. Classically, however, the term covers a few particular orders. Here it refers to Anoplura (lice), Siphonaptera (fleas) and Acari (mites and ticks).

The number of realized life strategies among small mammal ectoparasites is overwhelming. This thesis focuses on some details of a few of these tactics.

The thesis consists of five papers:

- I. Life-traits of ectoparasites on small mammals. (Manuscript)
- II. Environmental effects on the prevalence of small mammal ectoparasites. (Manuscript)
- III. The estival ectoparasitic burden of six small mammal species in northernmost Fennoscandia. (Manuscript)
- IV. Is ectoparasitic infestation a function of host size in small mammals? (Manuscript)
- V. Association, interaction and niche overlap. (Submitted)

Roman numerals in the following text refer to the above mentioned papers. The presentation of the material below is followed by a brief summary of the papers, together with some commentary notes.

1. The material

About 10,000 small mammals (Tab. 1) were collected in the late summers of 1965-1970 in northernmost Fennoscandia (Finland, Norway and Sweden) (Fig. I:1). The main part of the sampling was performed during the first three weeks of August. Multiple-catching live traps (type Ugglan Special) were used. They were usually emptied in the mornings. However, when the traps were set for another 24 hrs, they were also emptied in the evenings. The number of animals collected in day-time was small, mostly less than 10 % of the total catch (Andersson and Hansson 1966). Collected small mammals were put in separate polyethene bags, killed with diethylether and weighed with a spring balance (type Pesola, ± 0.5 g). Their reproductive status was determined and they were then preserved in a mixture of equal amounts of 80 % alcohole and 4 % formaldehyde. Fifteen small mammal species were sampled, six shrews, seven voles and two mice.

Table 1. Hosts and their distribution among species, sex, and reproductive stage. Material from five regions in northernmost Finland, Norway and Sweden, investigated in 1965-70. Individuals of unknown sex and/or repr. stage are excluded.

Species	males	females	juveniles	subadults	adults	post repr.	sum
<i>Sorex araneus</i> L.	2,465	2,084	4,089	0	460	0	4,549
<i>S. isodon</i> Turov	0	1	1	0	0	0	1
<i>S. caecutiens</i> Laxmann	129	117	222	0	24	0	246
<i>S. minutus</i> L.	32	27	43	0	16	0	59
<i>S. minutissimus</i> Zimmerman	1	0	0	0	1	0	1
<i>Neomys fodiens</i> (Pennant)	27	20	37	0	10	0	47
<i>Lemmus lemmus</i> (L.)	11	7	2	4	12	0	18
<i>Clethrionomys glareolus</i> (Schreber)	240	213	22	285	135	11	453
<i>C. rutilus</i> (Pallas)	664	524	200	523	463	2	1,188
<i>C. rufocanus</i> (Sundevall)	585	702	364	301	621	1	1,287
<i>Microtus agrestis</i> (L.)	216	252	133	126	205	4	468
<i>M. oeconomus</i> (Pallas)	226	263	52	316	101	20	489
<i>Arvicola terrestris</i> (L.)	1	1	0	2	0	0	2
<i>Micromys minutus</i> (Pallas)	1	0	0	0	1	0	1
<i>Mus musculus</i> L.	43	42	41	7	37	0	85
Sum	4,641	4,253	5,206	1,564	2,086	38	8,894

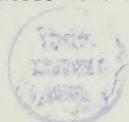
Table 2. Population density phases of rodents and shrews in five regions of northernmost Fennoscandia in 1965-70. (After Hansson et al., 1978).
l = low density years; i = increasing population; p = peak density years.

Region	1965	1966	1967	1968	1969	1970
Rodents						
I	i	p	l	i	p	l
II	i	p	l	l	i	p
III	i	p	l	l	i	p
IV	p	l	l	l	i	p
V	l	l	l	l	i	p
Shrews						
I	p	l	l	i	p	l
II	p	l	l	l	i	p

The host populations fluctuated in density during the period. The fluctuations were not synchronous for the shrew *Sorex araneus* and the vole populations over the total area. Low, increase and peak density years were designated on the basis of index trapping (Hansson et al. 1978). Pronounced fluctuations with 3-4 years rhythm in abundance were found for the rodents with peaks in 1966, 1969 and 1970. In region IV (Fig. 1:1) there were peaks in 1965 and 1970, while a peak year was observed in region V only in 1970. Insectivore fluctuations were pronounced only in regions I and II (Tab. 2).

In the laboratory some 67,000 arthropods were removed by hand from the fur of the small mammals. Ectoparasites were preserved in 80 % alcohol before mounted on slides and identified to sex and species. There were fifteen Siphonaptera, four Anoplura, nineteen mesostigmatic mite and one tick species. Lists of ectoparasites are given in papers II, III and IV. The ectoparasitic material has previously been reported by Brinck-Lindroth (1972), Edler and Mehl (1972), Edler and Mrciak (1975) and Nilsson (1974 a, b).

The genus *Hirstionyssus* was synonymized with *Echinonyssus* by Tenerio and Radvosky (1979). However, according to G.O. Evans (pers. comm.) one can retain *Hirstionyssus* as a subgenus for those species in which the dorsal spur of coxa II is not developed into a large hook-like process. For the sake of convenience the name of the subgenus *Hirstionyssus* will here be used instead of the generic name *Echinonyssus*.



The material was collected in the summer season. This is when the rodent population is building up and is subject to activities and movements that determine distribution and prepare for winter survival. The parasite population is part of the play: They have to adjust to the life-tactics of their hosts at the same time as they part the resources. The fact that the material is seasonally uniform facilitates comparisons from one year to the next. This is an important aspect since a main aim was to study whether the ectoparasites exhibit the same, or similar, yearly fluctuations as their host animals. On the other hand, taxonomists should not accept the lists of species as complete. There are species of e.g. fleas which appear in the winter season. Similarly, densities and relations between the parasite species may change with season. This should not detract from the value of assessing conditions during the season of main activity.

2. "To be or not to be" (I)

The life tactics of an ectoparasite should maximize the exploitation of either the host individual or the host population, since these are incompatible. Based on this dichotomy one can distinguish two main trends in the evolution of the ectoparasites: The representatives of the first one stay on the host and reproduce there, while those representing the other trend visit the host for short periods only and oviposit and develop their larvae off the host. Reproduction on the host is advantageous when the host individual constitutes a predictable environment, whereas reproduction off the host may be successful when the number of hosts can be forecasted. In addition, staying on the host minimizes the risk of not finding a host for the next blood meal, while reproduction off the host minimizes the risk of being eaten. Reproduction on the host predictably leads to iteroparity, reproduction off the host logically to semelparity (big bang reproduction).

These differences imply that the host population is a patchy environment where the patches are ephemeral. For parasites that reproduce on the host may the patchiness be very real; the transition areas between the individual hosts have become uninhabitable. This type of ectoparasite is called full-time parasite. Part-time parasites, then, are those that also include parts of the environment - their host's nests and/or runways - in their optimal habitats.

Three groups of ectoparasites (one full-time and two part-time) were recognized. 1) Species with narrow host preference spectra, whose population fluctuations follow the dynamics of the host populations. These species often infest their hosts heavily. The group is called the Anoplura-Laelapinae group. 2) Species characterized by moderate to broad host preference spectra with a time lag of one year between the population peaks of the host and the parasite and with low infestation level. This is the Siphonaptera-Haemogamasinae group. 3) A species group, with a moderate host spectrum, a time lag of two years between peak of host and parasite population fluctuations and with moderate infestation level. The only species of this group in the material is *Ixodes trianguliceps*.

The above classification of ectoparasites corresponds approximately with three of Camin's (1964) groups, i.e. a) host-dwelling, b) nest-dwelling and c) field-dwelling ectoparasites. Camin referred to three phases of ectoparasitic behaviour. In phase one the behaviour makes host encounters feasible, e.g. the movements of *Ixodes ricinus* L. larvae towards the top of low vegetation. The second phase includes the detection of the host and its climbing. An ectoparasite must detect a host within a distance that makes mounting possible. In phase three the ectoparasite is on the host locating the predilection places and penetrating the skin.

A part-time ectoparasite living outside the nest or runways of the hosts has to go through all these phases of behaviour to feed. A nest or runway ectoparasite usually has a host around and does not need the first phase. A full-time ectoparasite needs neither the first nor the second phase. Consequently, there are no morphological adaptations for these phases.

A typical full-time ectoparasite has a generation time shorter than the life expectancy of the host. A typical part-time ectoparasite has to find a host for the next meal, which is difficult when the host population has crashed. Thus, part-time ectoparasites as Trombiculidae are rare and the tick *Ixodes ricinus* is missing in the investigated area, where the small mammal populations fluctuate.

By waiting, a part-time ectoparasite may increase its chance of finding a new host. But waiting extends the generation time and has to be compensated for by an increased net reproductive rate in order to maintain the intrinsic rate of increase. The fleas have bypassed this drawback by having several generations with short generation times during the reproductive season alternating with one generation that survives to the next reproductive season.

3. The hardship of the secondary habitat (II)

The term "the secondary habitat of ectoparasites" was coined by Janion (1983) for the environment of the host animals. The term is used without any implicit ranking. The following notion is made: Can environmental influence on infestation figures be detected in part-time and/or full-time ectoparasites?

An easily measured infestation parameter, the prevalence, was used. Northernmost Fennoscandia was divided into subareas; four bio-geographical regions and twelve biotopes. Based on host species frequency in the subareas and the observed prevalence in the total area it was possible to calculate an expected prevalence in the subareas. If the observed prevalence in the subareas can be predicted in this way from the host species frequencies, then it is likely that the influence of the secondary habitat on the infestation rate is less than that of the hosts. In most cases there were no significant correlation coefficients between observed and expected prevalence in the haemogamasin mites and in most cases the correlation coefficients were statistically significant in the laelapin mites and the lice.

4. The majority of an ectoparasite population infest a minority of the host population

The spatial distribution of ectoparasites on their hosts has often been described as negative binomial (Crofton 1971, Randolph 1975, Robbins and Faulkenberry 1982), defined by an exponent k and the mean (Bliss and Fisher 1953). The distributions are often heavily skewed with most hosts not infested and they are sometimes very long-tailed (II). However, only a few ectoparasite species in northernmost Fennoscandia had a negative binomial distribution. *Laelaps clethrionomydis* was one. When hosts were arranged into clusters according to sex and reproductive status, the exponent k and the mean were similar in the different clusters for *L. clethrionomydis* (Fig. 1). For the louse *Hoplopleura edentula* (Fig. 2), however, there were great differences in these variables between the clusters.

It is likely that the infestation rate of a parasite is reflected in the spatial distribution of the parasitic population (Anderson and May 1978). Differences in infestation rate might therefore give differences in

the spatial variables k and the mean. Amalgamating clusters with such differences in infestation rates gives bi- or multimodal parasite distributions. Finding clusters of hosts with monomodal (e.g. negative binomial) parasite distribution might be a means of determining host groups with homogeneous infestation rates.

5. The exploiters' club(III)

Several papers on ectoparasites deal with single species and have shown that many ectoparasites have a clumped frequency distribution i.e. most individuals of one species aggregate on a few host specimens. The following questions then arose: are individuals of other ectoparasitic species attracted to the same host specimens? Or do they prefer hosts that are not previously infested? Can pairs of ectoparasitic species often occurring together be demonstrated?

The total estival ectoparasitic burden on six of the small mammal species from northernmost Fennoscandia were investigated. Of the shrew species, *Sorex araneus*, 51% of the specimens had no ectoparasites at all. Corresponding figures for the vole species varied between 4 and 27%. The median vole had, depending on species, 1 to 9 ectoparasites of 1 or 2 species. The maximum number of ectoparasitic species observed on approximately 10,000 small mammals was eleven. The number of ectoparasitic species was plotted against the total number of specimens on each host and the product-moment correlation coefficient was calculated. (Figs III:3-8). There was a significant, positive correlation between the number of ectoparasitic species and specimens on all host species. On hosts with extreme numbers of ectoparasites usually one species dominated. Pairs of ectoparasites were formed by species occurring together more or less often than could be expected by chance. The same pairs were, however, not repeatedly found in different subsamples of hosts.

Laelaps clethrionomydis

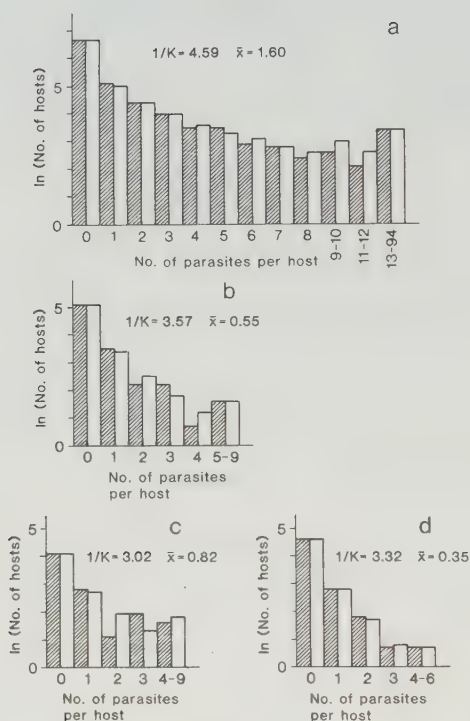
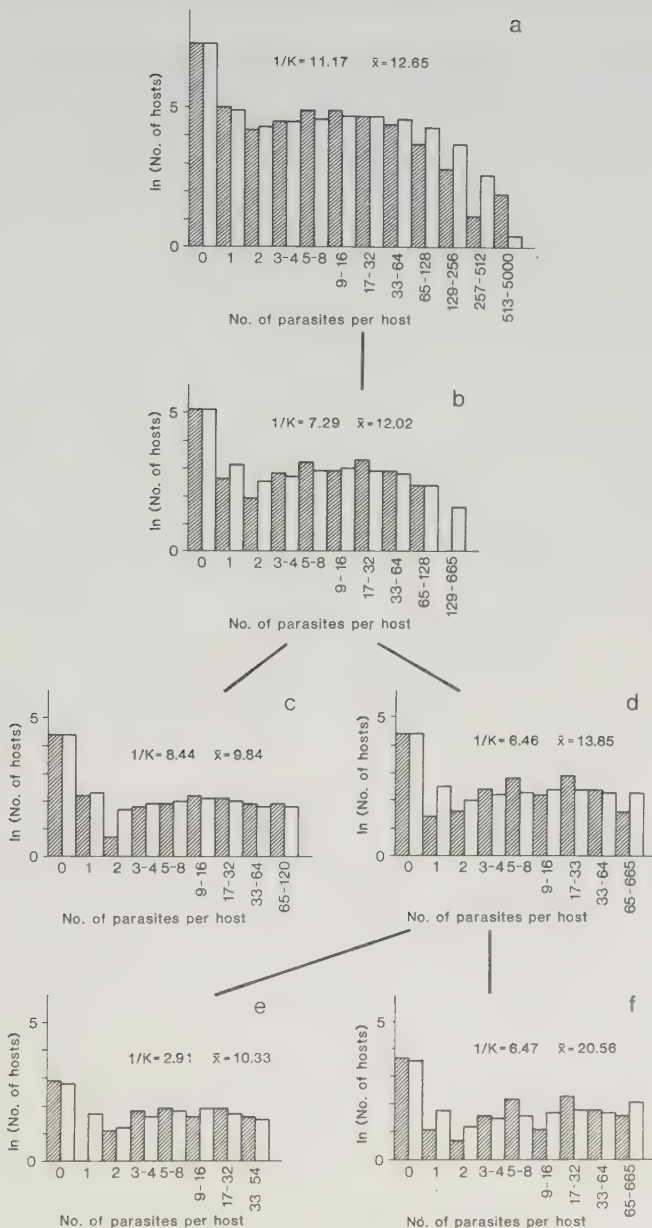


Figure 1. Identifying clusters of hosts with monomodal (e.g. negative binomial) parasite frequency distribution might be a means of determining host groups with homogeneous infestation rates. *Laelaps clethrionomydis* is an example of an ectoparasitic mite whose frequency distribution is similar in subclusters. N: number of hosts, n: number of parasites. a) Regions II + III + IV, all years, ♂♂ + ♀♀, all ages: $\chi^2_{[1]} = 9.25$, $p > 0.50$, N: 1,255, n: 2,009. b) Region II, 1966, ♂♂ + ♀♀, all ages: $\chi^2_{[2]} = 2.53$, $p > 0.10$, N: 216, n: 119. c) Region II, 1966, ♂♂, all ages: $\chi^2_{[1]} = 2.77$, $p > 0.10$, N: 91, n: 75. d) Region II, 1966, ♀♀, all ages: $\chi^2_{[1]} = 0.04$, $p > 0.50$, N: 125, n: 44.

Figure 2. There are differences in the frequency distribution variables of the louse *Hoplopleura edentula* in different subclusters. Amalgamating such clusters results in polymodality.

a) Regions II + III + IV, all years, ♂♂ + ♀♀, all ages: $\chi^2_{[20]} = 66.18$, $p < 0.001$, N: 2,300, n: 29,085. b) Region II, 1966, ♂♂ + ♀♀, all ages: $\chi^2_{[7]} = 14.66$, $0.05 > p > 0.01$, N: 300, n: 3,606. c) Region II, 1966, ♂♂, all ages: $\chi^2_{[7]} = 2.65$, $p > 0.50$, N: 137, n: 1,348. d) Region II, 1966, ♀♀, all ages: $\chi^2_{[7]} = 18.12$, $0.05 > p > 0.01$, N: 163, n: 2,258. e) Region II, 1966, ♀♀, juveniles: $\chi^2_{[3]} = 4.70$, $p > 0.10$, N: 52, n: 537. f) Region II, 1966, ♀♀, adults: $\chi^2_{[4]} = 9.43$, $0.10 > p > 0.05$, N: 82, n: 1,686.

Hoplopleura edentula



6. The numbers of ectoparasites: how to report them?

In papers I-IV the number of ectoparasites per host is discussed. At first sight this variable looks simple enough. It has, however, been dealt with in various ways. Often the value is given as the number of ectoparasites of one species divided by the number of hosts, species by species ($\bar{x}$) (George and Corbet 1959, Uchikawa 1967, Artz 1975). Such values are difficult to compare. Other authors have divided the number of ectoparasites by the number of infested hosts, $\bar{x}_{inf}$ (e.g. Edler 1973). Another mean, $\bar{x}_{tot}$, has been calculated by dividing the number of ectoparasites by the total number of hosts in the material (Randolf 1975, Nilsson and Lundqvist 1978).

The quantity $\bar{x}_{tot}$ is not recommended for ectoparasites with restricted host preferences, as it comprises entities that bring only little biological information to the reader, e.g. including the number of shrews into the denominator of a vole parasite. On the other hand, the distribution of the ectoparasites gives important information about the type of dispersal of the parasites (Anderson and May 1978). One important variable in this context is the number of hosts not infested but with the potential of being infested. These hosts are not included in $\bar{x}_{inf}$. Trying to avoid the limitations of $\bar{x}_{tot}$ and $\bar{x}_{inf}$ another mean, $\bar{x}_{cat}$, where cat stands for host category, was defined in paper I. In $\bar{x}_{cat}$ only the most common host-parasite combinations were considered, viz. those that comprised at least 90% of the parasite population.

The advantage of all the $\bar{x}$ values discussed above is that they are easy to envisage. They can also be used in e.g. cluster analysis (cf. paper I). The drawback is that parametric test statistics can not be used when comparing $\bar{x}$, since the ectoparasites are not normally distributed ($S^2 \neq \bar{x}$) and hence neither is the mean. In papers II and III the hosts were therefore classified according to their number of ectoparasites, and the distribution of the classes was tested with χ^2 -tests. The class width was chosen so that no expected value was less than five. Two or more distributions can be tested in this way, irrespective of their means and variances. This method gives no single infestation value. A combination of both methods is of course possible.

7. Are large animals infested by more ectoparasites than small ones? (IV)

Paper IV was influenced by the thoughts of Price (1980). He hypothesized that there is a positive relation between the number of parasites and the size of the host and he also cited work on the subject with examples from plants, birds and mammals. The hypothesis is in accordance with general island biogeography theory. To test the hypothesis we regressed the number of ectoparasites (species and specimens) on the size of small mammal hosts. The surface area (S) of each host was calculated as $S = W^{\frac{2}{3}}$ (W = weight of the animal).

A significant regression was found between the number of species, and specimens, and the size of the host. However, there was no significant regression between the number of species, or specimens, and the size of a specific host species, except for *Sorex araneus* during peak years. Generally, the regression for specific host species appeared to be bell-shaped, indicating that middle-sized hosts were the most heavily infested. It was noted that there was a significant regression between the number of full-time ectoparasite specimens and the size of *Clethrionomys rufocanus* individuals, but not so for part-time ectoparasites. This is in accordance with the presumptions of the island biogeography theory; a species invading an island should stay on the island and reproduce there. Full-time ectoparasites do that, but part-time ectoparasites are just foraging on the small mammal islands.

8. Species occur together in a habitat for two different reasons (V)

Two concepts of possible interference between two species were distinguished. Species are associated when they require similar resources (or habitats). They are less associated when their niches overlap only slightly and they are more associated the more similar their maximal specific net rate of population increase is at identical environmental conditions. Thus, association refers to habitat and resource preferences. Interaction, on the other hand, is the direct effect (positive or negative) on the specific population growth rate of one species by a sympatric species. The distinction between the two concepts is not always made explicit. When one has to measure the degree of co-occurrence, it is recommended to use a statistical method based on presence-absence data simultaneously with a method based on frequency data.

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One of the advantages of doing your thesis at an outstanding laboratory is that it finally ends up better than you deserve. Any quality in this thesis is a proof of that rule. That the animal ecology department of Lund University is excellent is very much the merit of professor Per Brinck. I thank him for the privilege I have had to work under his guidance. He also had to stand reading a number of versions of the manuscripts. He did that with great patience.

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LIFE-TRAITS OF ECTOPARASITES ON SMALL MAMMALS

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Abstract

A model of ectoparasitic life-traits is presented. An ectoparasite has to be good at either to migrate and to find a new host, or to stay on one host and produce its progeny during the lifetime of the host. Migration is facilitated by utilizing many host species and by waiting for the next host which prolongs the generation time. Staying on the host is facilitated by shortening the generation time. Migrating ectoparasites are thus expected to have wide host preference spectra and long generation times and sedentary ectoparasites to have narrow host preference spectra and short generation times.

Population parameters of 27 ectoparasitic species (fleas, lice, mesostigmatic mites and one ixodid tick species) on cyclic small mammal populations were investigated and a cluster analysis was performed. Three groups of ectoparasitic life-traits were discernible. 1) Narrow host preference spectra, no time lag between host and parasite peak abundance which indicates short generation times and heavy infestations of the hosts; the Anoplura-Laelapinae group. 2) Moderate-wide host preference spectra, one year time lag between host and parasite peak abundance which indicates long generation times, and low infestation; the Siphonaptera-Haemogamasinae group. 3) Moderate host preference spectrum, two years of time lag between host and parasite peak abundance, and moderate infestation; *Ixodes trianguliceps* was the only member of this group.

Ectoparasites, such as Trombiculidae mites and the tick *Ixodes ricinus*, which are not confined to small mammals, were missing or very rare on the cyclic small mammal populations. This was predicted by the model.

Introduction

A parasite has three alternatives to reproduce: i) "here and now", ii) "here but later" and iii) "elsewhere and later" (Southwood 1977). The restraints of these options are "how long will a specific, suitable patch last" and "what are the chances of finding another patch?" According to alternatives i) and ii) (without migration) the parasite must produce its progeny within the life-span of the host. For a successful reproduction the third alternative postulates that the parasite finds a new host. The chance of doing so comprises at least two elements: a) a specific host-finding property of the parasite species, and b) the number of available hosts.

In this paper a simple model of ectoparasitic life-traits is formulated. The model is based on the fact that some ectoparasites are one-host parasites, while others have adapted a strategy of recurring host exchange. The strategies are chiseled out by the evolution within the ectoparasitic population but are also a result of host properties and host population characteristics.

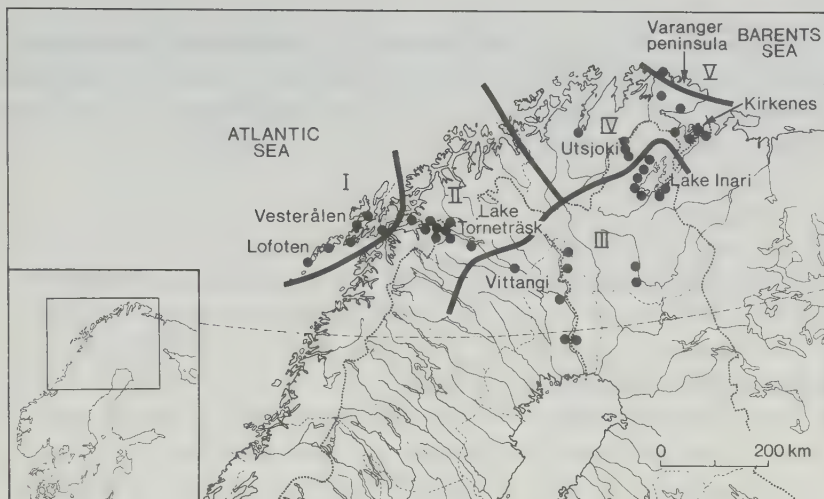


Figure I:1. Northernmost Fennoscandia divided into five regions I-V on biogeographical basis (After Hansson et al. 1978.) Localities investigated are indicated by dots.

Material

The small mammals

Eleven small mammal species, of more than 10 specimens, were used in this analysis (Tab. thesis 1).

On a bio-geographical basis the investigated area was divided into five regions [see also Hansson et al. (1978) and paper II] (Fig. I:1).

Ectoparasitic species with 50 or more specimens are dealt with here, which leaves a total of 66,083 parasites of 27 species (c.f. Tab. III:1 and Fig. I:5.

The model

To reproduce according to alternatives i) and ii) in the Introduction, it is necessary that the generation time of the parasite, ρ , is shorter than the duration of the patch being favourable for the parasite, H . This can be expressed as an inequality:

$$H/\rho \geq 1 \quad (I:1)$$

where H is the average life-span of a host individual.

The two elements of successful reproduction "elsewhere", according to alternative iii) can be denoted by m , the specific host-finding intrinsic property of the parasite, and $N_{(t)}$ the number of hosts at time t . The chance of successful reproduction can then be formulated as:

$$p = m \cdot N_{(t)} \quad (I:2)$$

Among the parameters introduced H and $N_{(t)}$ are properties of the host population and can not be altered by selection among the parasites.

The unpredictability of H and $N_{(t)}$

In a small mammal population, the life-span of an average individual, H in (I:1), is highly unpredictable and varies greatly with the time of birth, sex and cyclic phase (Myllimäky 1977, Erlinge et al. 1983, Gliwicz 1983). The number of available hosts, $N_{(t)}$ in (I:2), varies with the season (Fig. I:2). Furthermore, in a cyclic population the number varies with the cyclic phase.

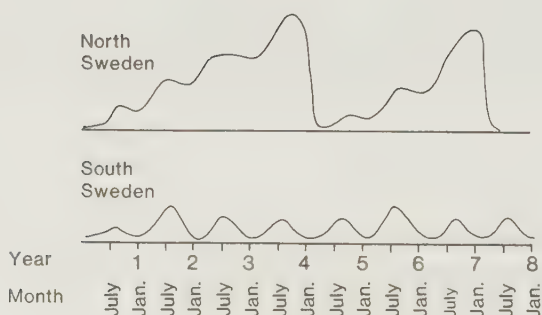


Figure I:2. Differences in population dynamics of a cyclic and a non-cyclic small mammal population. (After Hansson 1971.)

Parasite generation time

Pielou (1977) defined T as a generation time for populations with non-overlapping generations:

$$T = \frac{\ln R_0}{r} \quad (I:3)$$

where R_0 is the net reproductive rate and r is the intrinsic rate of natural increase. She also gave a definition of the generation time for populations with overlapping generations.

However, in this paper, I will use ρ as a symbol for the generation time of the ectoparasites for both overlapping and non-overlapping generations. Doing so is justified when r is "sufficiently small" (Pielou 1977).

Estimating the host-finding ability

The host-finding ability of an ectoparasite is denoted by m in (I:2). There are at least three ways for an ectoparasitic species to increase m by means of natural selection: i) to increase the ability to resist starvation and drought, ii) to trace host by means of special adaptations and iii) to increase the host spectrum. If any small mammal encountered by a searching ectoparasite can serve as a host, then searching time is shortened. This ability is important when host animals are rare as during low population density phase. In this paper an index of the host preference spectrum is used as an estimator of m .

Methods

Three variables of parasite-host interactions were studied, 1) on an interval scale and 2) and 3) on an ordinal scale: 1) the breadth of the host spectrum, B_c , 2) $\Delta B = B_{low} - B_{peak}$, the change in B with decreasing host abundance (actually the sign of dB/dN), 3) $\Delta \bar{x} = \bar{x}_{low} - \bar{x}_{peak}$, the change in parasite mean infestation when the host population fluctuates from peak to low density years (the sign of $d\bar{x}/dt$).

The breadth of the host spectrum

The niche breadth, B, defined by Levins (1968) was used to measure the host preference spectrum.

$$B_j = \frac{1}{\sum_{i=1}^k q_i} \quad (I:4)$$

where k is the number of host species and

$$q_i = (P_i)^2 \cdot (P_T)^{-2} \quad (I:5)$$

Here P_i is the number of parasites on the i:th host species. P_T is the total number of parasites of species j.

This B value illustrates a parasite's host preference spectrum in a specific situation, given the host species frequencies, and was used to calculate ΔB , the change of host preference spectrum from host peak year to low year.

However, to obtain a B value less dependent on the specific environment (the frequency of different small mammal species differed between years and regions), a B_c value based on a standardized host material was used; Thus, substitute (in I:4)

$$q_i = \left(\frac{P_i}{N_i}\right)^2 \cdot (P_T)^{-2} \quad (I:6)$$

where N_i is the number of hosts of the i:th species. The B_c value was calculated over all years.

The mean number of parasites per host

From the variation in the host preference spectrum (B_c) three main categories of host selection among ectoparasites were discernible (Tab. I:1). Category 1 comprised ectoparasites that occurred on one or at most two host species, most often of the same genus. In category 2 were ectoparasites with a broader host spectrum, where the hosts often belonged to different genera. Two groups were distinguished; 2:1 comprised the vole ectopa-

Table 1: Ectoparasites (species with more than 50 specimens collected) from small mammals in northernmost Fennoscandia in 1965-70. Arranged according to increasing host preference spectrum, B_c . n = number of specimens; cat = host preference category, 1 = specialists, 2:1 = vole and 2:2 = shrew ectoparasites, and 3 = generalists. In this table the full subspecies names of the fleas are given. Only species names are used in the text and figures.

Species	n	B_c	ΔB	cat.
<i>Polyplax serrata</i> (Burmeister)	78	1.00		1
<i>Leaelaps clethrionomydis</i> Lange	2,267	1.21	(²)	1
<i>Polyplax borealis</i> Ferris	757	1.36	-	1
<i>Myonyssus ingricus</i> Bregetova	70	1.41	-	1
<i>Hyperlaelaps microti</i> (Ewing)	1,328	1.44	(²)	1
<i>Hoplopleura edentula</i> Fahrenholz	35,009	1.82	-	1
<i>Peromyscopsylla b. bidentata</i> (Kol.)	91	1.98	-	1
<i>Leaelaps hirsutis</i> Koch	4,866	2.07	-	1
<i>Hoplopleura acanthopus</i> (Burmeister)	1,437	2.12	-	1
<i>Hirstionyssus talpae</i> Zenskaya	637	2.53	+	2:2
<i>Palaeopsylla soricis</i> s.l. (Dale)	3,381	2.62	-	2:2
<i>Rhadinopsylla integella</i> Jordan & Rothschild	68	2.99	-	2:1
<i>Megabothris calcarifer</i> (Wagner)	168	3.26	(⁺)	2:1
<i>Haemogamasus nidiformis</i> Bregetova	233	3.34	+	2:1
<i>Hystriochopsylla o. orientalis</i> Smit	453	3.35	+	3
<i>Peromyscopsylla silvatica</i> (Weinert)	330	3.36	+	2:1
<i>Haemogamasus horridus</i> Michael	152	3.61	-	3
<i>Corrodopsylla birulai</i> (Ioff)	811	3.93	-	2:2
<i>Hirstionyssus isabellinus</i> (Oudemans)	4,262	4.04	-	2:1
<i>Aemphipsylla s. sibirica</i> (Wagner)	887	4.64	+	2:1
<i>Amalareus penicilliger pedias</i> (Rotsch.)	2,282	5.05	-	2:1
<i>Ixodes trianguliceps</i> Birula	2,259	5.17	-	3
<i>Megabothris rectangulatus</i> (Wahlgren)	1,665	5.54	-	2:1
<i>Haemogamasus nidi</i> Michael	477	5.59	-	3
<i>Ctenophthalmus u. uncinatus</i> (Wagner)	242	6.08	-	3
<i>Haemogamasus aebulans</i> (Thorell)	963	6.37	-	2:1
<i>Eulaelaps stabularis</i> (Koch)	410	7.34	-	3

parasites (on genera *Clethrionomys* and *Microtus* and 2:2 comprised the shrew ectoparasites (on genera *Sorex* and *Neomys*). Ectoparasites of category 3 had no distinct preference and were therefore considered to be true generalists.

For calculating the mean number of ectoparasites $\bar{x}_{cat}$ (Thesis, section 6), was used:

$$\bar{x}_{cat,i} = \frac{\text{The number of parasites of species } i \text{ found on hosts preferred by the species}}{\text{The total number of specimens of host species preferred by parasite species } i}$$

The preferred hosts of category 1 are the host species on which most specimens were found. Of category 2 the preferred hosts were voles, or shrews, and of category 3 no distinct preferences were observed. Categories were chosen such that at least 90% of all specimens of species i were included in $x_{cat,i}$.

When studying changes in x_{cat} with changing host abundance only timelags of one year could be observed, since the material was gathered by yearly collecting.

Cluster analysis

A cluster analysis (BMDP Statistical Software P2M) was performed on the material to form clusters of cases based on more than one variable. Initially every single species was considered as a separate cluster. The computer programme then joined cases and/or clusters of cases in a stepwise process until all cases were combined into one cluster. The algorithm used the distance between centroid clusters as a criterion for joining (amalgamating) clusters. The variables used in this analysis were as follows: The B_c value of each ectoparasitic species calculated over all years (interval scale), the changes in B with decreasing host abundance (ΔB , ordinal scale), the prevalence of each ectoparasitic species over all years and x_{cat} over all years (the two later both on ratio scale).

Results

The four Anoplura species all ranked among the nine lowest B_c values (Tab. I:1). Here were also found the four mite species in the subfamilies Laelapinae and Myonyssinae. **Peromyscopsylla bidentata** was the only flea species (rank 7) among the nine lowest B_c values. The remaining 18 species (ranks 10 to 27) were mites of the subfamilies Haemogamasinae and Hirstionyssinae, the tick **Ixodes trianguliceps** and fleas.

In 14 out of 22 cases (in the remaining species the material was too small for analysis) $\Delta B < 0$, i.e. the host preference spectrum was narrower in low years than in peak years (Fig. I:3). In table I:1 the sign of $\Delta B/\Delta N$ is given for 26 species. In the absence of a good statistical method for testing the significance of the changes, general trends were considered more important than specific examples. Eight of nine category 1 species with the lowest B_c values restricted their host preferences when hosts

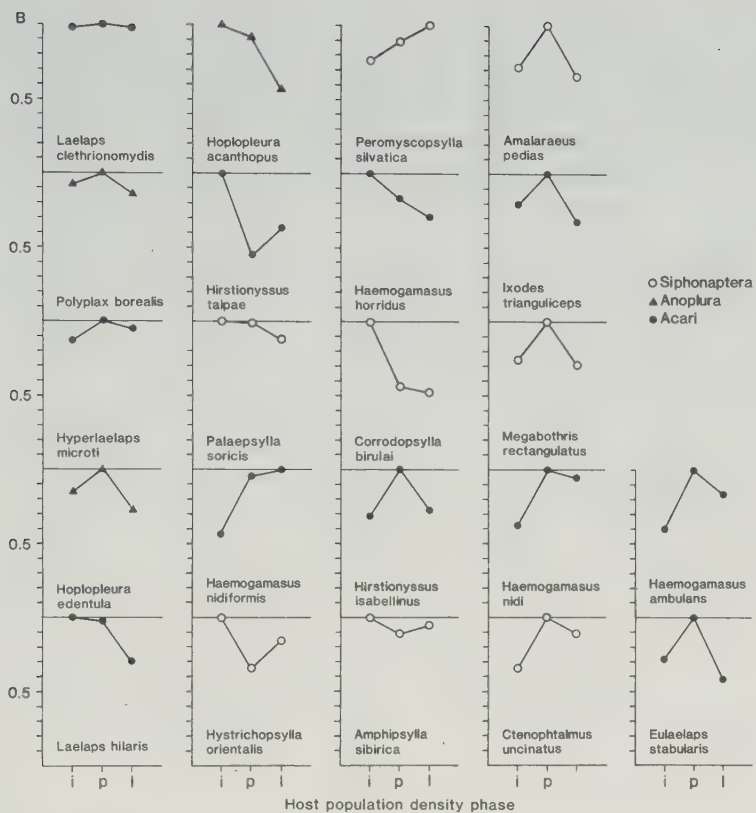


Figure I:3. Changes in the host-breadth spectrum value (B) when the host population crashes from a peak year to a low year. The values are standardized so that the largest B value is 1, and smaller values are expressed as fractions of the largest; i = increase years; p = peak years; l = low years.

became sparse in low years. The changes were, however, very small for two species, *Laelaps clethrionomydis* and *Hyperlaelaps microti*. Of the categories 2 and 3, species with moderate B_C values, ranks 10-16, five out of seven broaden their host spectrum. Ten of the eleven species with the highest B_C values, ranks 17-27, restricted their host spectrum in low years compared to peak years.

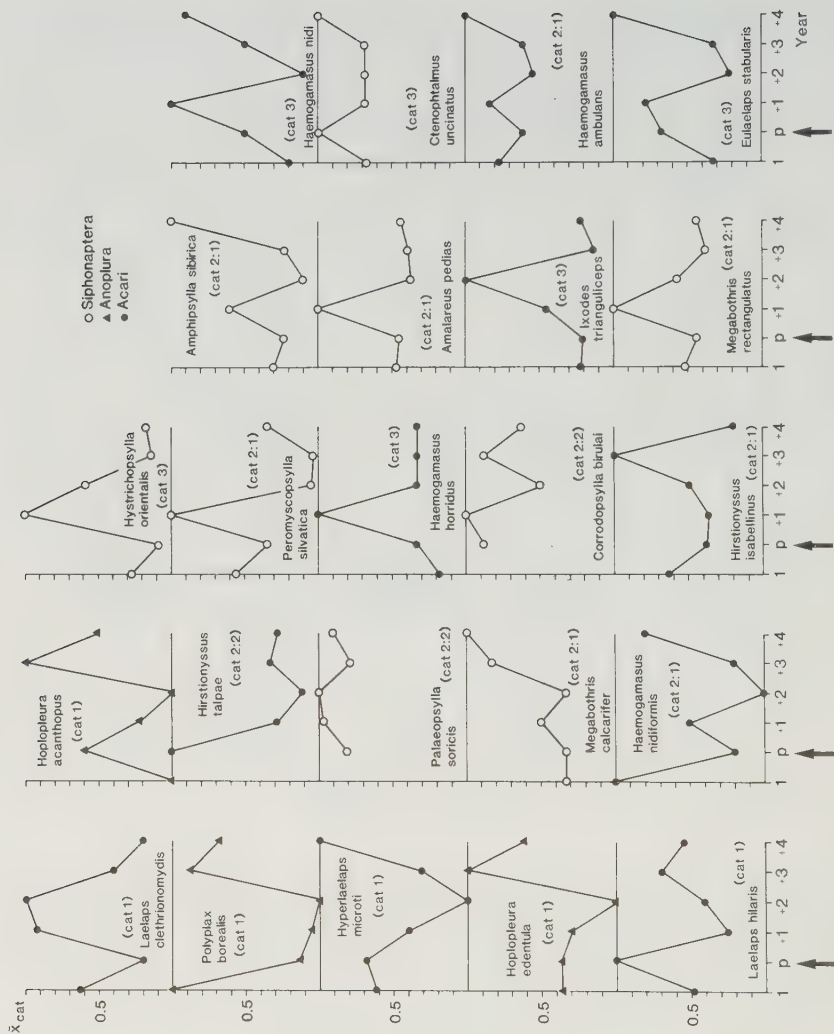


Figure I:4. Changes in $\bar{x}_{cat}$ when the host population crashes from a peak year to a low year. For shrew parasites (category 2:2) the figures for regions I and II are calculated, for other parasites also region III is included. In these areas the shrews had a peak density year in 1965 and voles in 1966. p = peak year. The values are standardized so that the largest $\bar{x}_{cat}$ value is set to 1 and smaller values as fractions of the largest.

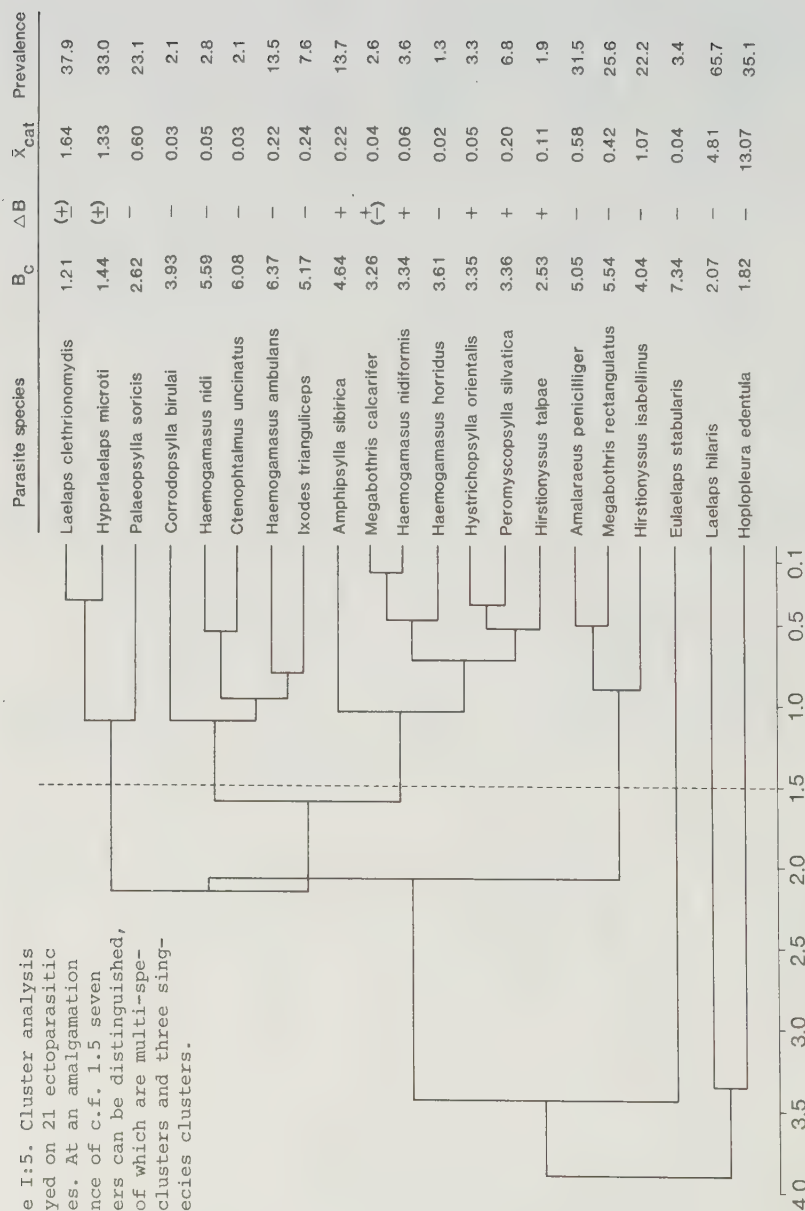
Three types of changes in ectoparasitic density from host peak years to host low years can be expected (Fig. 1:4). 1) A less than one year time lag between the peak of host abundance and the response of the ectoparasites. This can be manifested as an apparently simultaneous peak of host and ectoparasitic abundance. 2) A one year time lag and 3) two or more years of time lag between host peak and ectoparasitic response. In figure 1:4 the variation in density (x_{cat}) is illustrated for the 23 most abundant ectoparasitic species. For species of group 2:2 (shrew specialists) collections from regions I and II (Fig. 1:1) were used, while for the other categories also hosts from region III were considered. In these regions shrews had peak years in 1965, and voles in 1966. Due to the low number of hosts during low years only six of the nine specialist species could be analysed. They showed considerable differences between host peak and low density years. Five of them had a somewhat similar development with low means when the host population was low. Four had in addition peak densities in phase with host populations. The louse *Polyplax borealis* and the mite *Laelaps clethrionomydis* had both low densities at host peak years.

L. clethrionomydis diverged from the specialist pattern also in host low years by being most abundant both one and two years after the host peak year. The densities of the ectoparasites in categories 2 and 3 usually varied less strongly (Fig. 1:4). In eight flea species out of nine there was a more or less pronounced peak of density the year after the host peak year. The exception was *Ctenophthalmus uncinatus* which maintained a notably steady population from year to year. The mite species of the subfamilies Haemogamasinae (genera *Haemogamasus* and *Eulaelaps*) had the same type of population development as the fleas. The mite *Hirs-tionyssus talpae* was in phase with the population density cycle of its hosts. The tick *Ixodes trianguliceps* had a two years' time lag between peaks of abundance of host and parasite (Nilsson 1974b). The mite *Hirs-tionyssus isabellinus* seemed to have a three years' time lag. Whether this was a true population dynamic feature is uncertain.

A cluster analysis cannot be performed on species with missing variable values. Therefore only four out of the nine species of category 1 were included. Likewise one of the twelve category 2 species was excluded. Nevertheless, the results from the analysis are worth considering.

At a moderate amalgamating distance, e. g. 1.5 (Fig. 1:5) four clusters of altogether eighteen ectoparasitic species were found. In addition there were three species that could not be placed in any of these clusters. Two

Figure 1.5. Cluster analysis employed on 21 ectoparasitic species. At an amalgamation distance of c.f. 1.5 seven clusters can be distinguished, four of which are multi-species clusters and three single species clusters.



middle clusters were discernible. The cluster *Corrodopsylla birulai* - *Ixodes trianguliceps* comprised species with low mean number of ectoparasites per host and low prevalence. They all had negative ΔB . In the cluster *Amphipsylla sibirica* - *Hirstionyssus talpae* the species had low means and prevalences, but most of them had positive ΔB . *Haemogamasus horridus* was the only exception with negative ΔB . The clusters flanking the middle clusters were both characterized by fairly high mean number of ectoparasites per host, high prevalence and negative ΔB . The cluster *Laelaps clethrionomydis* - *Palaeopsylla soricis* had low B_c values, while the cluster *Amalaraeus penicilliger* - *Hirstionyssus isabellinus* had high B_c values. The two middle clusters comprises ectoparasites of categories 2 and 3. These were mites of the genus *Haemogamasus* and fleas with one year time lag between host and parasite peak density. Species of category 1, the specialists, were found in the flanking cluster with low B_c values and two of them in the single species clusters. These had great amalgamating distances from other clusters; *Laelaps hilaris* due to the extreme prevalence and *Hoplopleura edentula* to the extreme mean of parasites per host. The mite *Eulaelaps stabularis* was the third single species cluster. In this species the single species cluster was due to extreme B_c and ΔB values, i.e. host preference rather than infestation level. In host peak years this mite was a pronounced generalist, but in low years the shrew *Sorex araneus* became a most important host.

Life-traits

Based on the category classification, cluster analysis, and the time lag between host and parasite peak density, three groups of life-traits were discernible. These groups comprised taxa of different levels.

The first group was distinguished by a narrow host spectrum, by high or extremely high infestation levels (expressed as mean and/or prevalence) and by no time lag between host and parasite abundance. The group includes Anoplura and the subfamily Laelapinae of the mesostigmatic mites.

The second group was the largest one and characterized by moderate to high positive or negative B_c values, low infestation and a one year time lag between peak years of density. Species of both categories 2 and 3 belonged to the group. The group comprised species of Siphonaptera and the subfamily Haemogamasinae among the mites.

The tick *Ixodes trianguliceps* alone constituted the third group. The group was based on the fact that *I. trianguliceps*, besides being the only tick, was the only species with a two years' time lag. This ectoparasite was a generalist (actually the larvae infested shrews and the adult voles, vide Nilsson 1974b) with low infestation level, moderate B_C and negative ΔB .

The genus *Hirstionyssus* was not easily included in this arrangement. The species had moderate B_C values, like the Siphonaptera - Haemogamasinae group, but differed from this in their peak of density which was in phase with the host population as found in the Anoplura - Laelapinae group.

Discussion

From equation (1:3) we know that there is a direct proportionality between r , the intrinsic rate of natural increase and the inverse value of ℓ the generation time, while the proportionality between r and R_0 , the net reproductive rate is logarithmic. Thus, r is more sensitive to changes in generation time than to changes in the number of offspring.

In this paper the breadth of the host spectrum, B_C , was used as an estimator of m , the host finding ability of the parasite. The prerequisite for this is that the parasite does not use any special means to find a particular host species, which should drastically reduce B_C at the same time as m should rise. Such a mechanism is known for e.g. the African tick species *Ixodes (Afrixodes) neitzi*. The antelope *Oreotragus oreotragus* uses a secretion as an intraspecific communication. But this secretion also attracts ticks (Rechav et al. 1978) which results in a positive effect on m . In such a case B_C does not work as an estimator of m . However, there are no reports supporting the assumption that such particular hostparasite relationships exist in small mammals in Scandinavia.

Two of the variables classifying the ectoparasite populations, can only take one of three integer values. This is the time lag between peak of host and parasite density (0,1 or 2) and the host preference category (1,2 or 3). Because of this, these two variables were not used in the cluster analysis, although they were considered important for classifying the ectoparasites.

Anoplura and Laelapinae are characterized by reduced generation time, ρ , and benefit from the direct proportionality between r and $1/\rho$ in (I:3). Reducing the generation time is a way to increase r without increasing R_0 . There are only few reports on the reproduction of terrestrial ectoparasitic arthropods. The human head-louse, *Pediculus humanus* var. *capitis* (L.), produces about 120 larvae per female (Nuttall 1917), Brinck-Lindroth et al. 1984). Marshall (1981) gives further references: *Haematopinus eurysternus* (Nitzsch) (world-wide on cattle), 24 (maximum) offspring per female, and *H. tuberculatus* (Burmeister) (on buffalo in Asia) mean offspring per female 73 (93 as a maximum). Edler and Solomon (1979) reported that the laelapine mite *Laelaps agilis* Koch is ovoviviparous. It is likely that this also applies to other *Laelaps* (and probably also *Hyperlaelaps*) species. There is, however, no detailed information on the reproductive output of *L. agilis*.

The second group (Siphonaptera-Haemogamasinae) had typically a one year time lag, which indicates a longer generation time. This implicates that R_0 should be relatively high. Marshall (1981) gave two references: *Echidnophaga myrmecobii* Rothschild (on small mammal in Australia) produces 170 offspring per female as a mean (250 as maximum) and *Pulex irritans* L., the human flea, produces as a maximum 448 offspring per female. According to Osbrink and Rust (1984) the cat flea, *Ctenocephalides f. felis* (Bouché) lays a life-span average of 158.4 eggs per female (432 maximum).

It seems that the fleas can bypass the drawback of a high R_0 by producing one or more generations during a reproductive season (Brinck Lindroth pers.comm., Darskaya and Suvorova 1984). During the reproductive season the generation time is short, one to three months (Marshall 1981). In this way the fleas can increase r but still keep R_0 reasonably low. This phenomenon is known from many other taxa, e.g. aphids and various other pest insects. If it applies to haemogamasine mites is not known.

Ixodes trianguliceps which in this material constituted the third life-trait group, had a long generation time, several years according to Nilsson (1974b). To compensate for such a long generation time Ixodidae ticks usually have a high R_0 . *Ixodes ricinus* (L.) (on small mammals in Europe) lays about 2000 eggs per female (Arthur 1962). The reproductive output of *I. trianguliceps* is not known, but may be less than that of *I. ricinus*, because of the close association to the small mammal hosts (Nilsson 1978).

In an evolutionary perspective different life-traits of ectoparasites on small mammals can be distinguished. At one extreme there are parasites with reduced average life-span, ρ in (1:1). In this case the host individual as an environment is relatively stable, since $\rho < H$. This is so even if $N_{(t)}$ is fluctuating. However, by shortening the generation time, the parasites become heavily dependent on the host and can not survive for long outside the host. They are transferred between hosts by direct contact. It is likely that the number of intraspecific encounters between hosts are greater than interspecific encounters. This makes, apart from physiological adaptations, the host spectrum (B) narrow.

Other ectoparasites have a large m , i.e. the ability to find new hosts. For these parasites the habitat is not only the host but also the areas between the hosts. The advantage of this tactic is the reduced risk of the unpredictable and short average life-span of the hosts, H . But there are at least two disadvantages. First, these parasites have to find new hosts, often several times during a life time; $N_{(t)}$, the number of hosts at time t , must be sufficiently high ($>1/m$) and $N_{(t)}$ can not be changed by selection among the parasites. $N_{(t)}$ is, on the contrary, an ecological variable and as such exposed to rapid alterations, while m is predominantly an evolutionary variable. Optimally, from the parasite's point of view, there should be a correlation between $N_{(t)}$ and $N_{(t+1)}$ which is not always the case in a cyclic host population. Secondly, increasing m by prolonging the time interval between meals, also prolongs the generation time. Increasing r , the intrinsic rate of natural increase, at these circumstances, involves a growing R_0 , the reproductive output. Furthermore, R_0 is only logarithmically proportional to r .

Thus, it seems that parasites that concentrate on increasing the ability to find new hosts are dependent on an ample and predictable access to hosts. Such a steady level can not be found in a cyclic host population. This is supported by the fact that the number of Trombiculidae mites on small mammals decreases towards the north. Members of this mite family are parasitic only as larvae, while the adults are free-living predators. Similarly the tick *Ixodes ricinus*, a common ectoparasite throughout Europe, is missing in the north where the small mammal populations are fluctuating. Also this species is heavily dependent on small mammals in its larval stage.

ENVIRONMENTAL EFFECTS ON THE PREVALENCE OF SMALL MAMMAL ECTOPARASITES

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Abstract

It is hypothesized that part-time ectoparasites on small mammals disperse via the habitat, while full-time parasites spread throughout the host population by direct contacts between host animals. The hypothesis is tested by analysis of the effects of the natural environment on the prevalence. Two possible mechanisms of such an effect are also studied, i.e. host selection and its changing with host frequency, and parasite immigration and reproduction rates as reflected by the frequency distribution patterns on the hosts.

The prevalence of part-time ectoparasites (subfamily Haemogamasinae) could not be predicted on the basis of host species frequencies during different environmental conditions, while prediction was possible for full-time parasites (Anoplura and subfamily Laelapinae), with the exception of one louse species. Species of subfamily Haemogamasinae were more catholic in host selection than species of Anoplura and subfamily Laelapinae. The haemogamasin mites changed host species to a greater extent than did Anoplura and Laelapinae. All haemogamasin mites had short-tailed frequency distribution patterns and all Anoplura and Laelapinae, except one mite species, had long-tailed frequency distributions. The hypothesis could not be rejected on the basis of these results.

Introduction

Lundqvist (thesis, section 2) discussed a dichotomy in the evolution of ectoparasites, into one group called full-time parasites which reproduce on the hosts. Another group was called part-time parasites since they abide the hosts for only short periods, and spend most of their time in the environment off the hosts. This evoked the following notion: Part-time parasite populations should be more influenced by the secondary environment (Janion 1983) than full-time parasites, whose conditions are solely set by the hosts. We will test this prediction by measuring the difference between observed and expected prevalences (the percentage of the infested host population) of the ectoparasites in different environments. Two effects of the environmental influence on the ectoparasite population are also studied, i.e. changes in host preference and frequency distribution of the parasites on the hosts.

Within the mite family Laelapidae, subfamily Laelapinae represents full-time parasites, while subfamily Haemogamasinae represents part-time parasites. Subfamily Hirstionyssinae was placed between these two life-trait groups by Lundqvist (paper I). Here we include the Anoplura species among the laelapin mites.

Material

Study area

The northernmost parts of Finland, Norway and Sweden are surrounded by the Atlantic and the Barents Sea (Fig. I:1). Even a slight altitudinal or longitudinal difference gives drastic effects on climatic conditions at these northern latitudes. Hence, there are relatively mild regions at the Atlantic coast in the west, an inland taiga and a coastal tundra close to the Barents Sea in the east.

The area was divided into five regions based on geography, vegetation (Hämet-Ahti 1963) and small mammal characteristics (Hansson et al. 1978). In region V only 72 mammals were collected; a number considered too small for our analysis. Host and ectoparasite material from this region was used only for calculating the expected prevalence in the total area and in the biotopes (see Methods).

Region I. The Lofoten and Vesterålen islands. Comparatively mild climate. Submaritime birch forests and relatively dry oligotrophic bog land.

Region II. The Scandinavian mountain range between the Norwegian coastal line and the eastern part of Lake Torneträsk. Subalpine birch forests and oligotrophic mires in the low and middle alpine belt.

Region III. Northernmost Sweden (Vittangi) and northern Finland (Lake Inari). Taiga with spruce and pine forests.

Region IV. Northernmost Finland (Utsjoki) and Norway (Kirkenes), close to the Barents Sea. Subalpine climax forests and eutrophic mires in low and middle alpine belts.

Region V. The coast of the Varanger peninsula at the Barents Sea, northernmost Norway. Dwarf-shrub communities.

Biotopes

The localities used for trapping were classified according to dominating plants (Tab. II:1).

1. Poor birch forest. Tree layer of *Betula pubescens* ssp. *tortuosa*.
2. Rich birch forest. Tree layer of *B. p. tortuosa*.
3. Swampy spruce forest. Tree layer of *Picea abies*.
4. Poor pine forest. Tree layer of *Pinus silvestris*.
5. Bilberry-pine forest. Tree layer of *P. silvestris*, field layer with *Vaccinium myrtillus*.
6. Mixed swampy forest. Tree layer with *B. p. tortuosa*, *Picea abies* and *Pinus silvestris*.
7. Willow shrub land. Shrub layer of *Salix* spp.
8. Mire edge. Shrub layer of *Salix* spp., *B. p. tortuosa* and *Pinus silvestris*.
9. Mire. Bottom layer of *Sphagnum* spp.
10. Hay meadow. Field layer with grasses.
11. *Empetrum*-*Betula nana* heath. Field layer of *Empetrum hermaphroditum* and *Betula nana*.
12. Close to buildings and refuse tips. Shrub layer of *Salix* spp. and *B. p. tortuosa*.

Small mammals and their ectoparasites

Host species of more than 20 specimens, were used in this analysis (cf. Tab. Thesis:1). The lowest admitted number of the ectoparasitic species was 70 (Tab. II:2).

Methods

The observed prevalence of an ectoparasitic species was compared with the expected value. The expected prevalence in a subarea (region or biotope) was calculated from the observed prevalence in the total area and the frequency of the hosts in the subarea. If a parasite population infests 10% of a certain host species in the total area and the host species constitutes 10 % of the small mammals collected in the subarea the expected prevalence will be 1 %.

Table II:1. Host animals collected in 12 biotopes and 5 regions in northernmost Finland, Norway and Sweden 1965-70.

	R	E	G	I	O	N	
	1	2	3	4	5		Sum
Biotope							
Poor birch forest	1,638	1,372	286	244	0		3,540
Rich birch forest	1,045	894	42	978	0		2,959
Swampy spruce forest	0	0	156	0	0		156
Poor pine forest	0	0	453	0	0		453
Bilberry-pine forest	0	0	208	0	0		208
Mixed swampy forest	0	0	114	25	0		139
Willow shrub land	0	184	35	0	15		234
Mire edge	13	0	20	76	0		109
Mire	128	2	16	32	0		178
Hay meadow	0	0	633	223	0		856
<i>Empetrum-Betula nana</i>							
heath	0	38	0	44	57		139
Close to buildings and							
refuse tips	137	260	42	0	0		439
Sum							9,410

Thus, the expected prevalence of the parasite species k in the subarea i was calculated as:

$$\frac{1}{100} \cdot \sum_{j=1}^M \left[n_{ij} \cdot \frac{10,000}{N_i 100} \cdot \frac{m_{jk} 100}{N_j} \right] \quad (\text{II:1})$$

where:

M = number of host species,

m_{jk} = number of host animals of species j infested by parasite species k ,

n_{ij} = number of host animals of species j in subarea i ,

$N_i = \sum_{j=1}^M n_{ij}$, total number of host animals in subarea i ,

$N_j = \sum_{i=1}^S n_{ij}$, total number of host animals of species j ,

s = number of subareas.

Table II:2. Lice and Laelapidae species with 70 specimens or more collected from small mammals in northernmost Finland, Norway and Sweden in 1965-70.

species	males	females	juveniles	Sum
ANOPLURA				
<i>Hoplopleura acanthopus</i> (Burmeister)	372	867	181	1,420
<i>H. edentula</i> Fahrenholz	9,620	20,589	1,283	31,492
<i>Polyplax borealis</i> Ferris	158	510	89	757
<i>P. serrata</i> (Burmeister)	7	67	4	78
ACARI				
<i>Eulaelaps stabularis</i> (C.L. Koch)	7	400	0	407
<i>Haemogamasus horridus</i> Michael	42	29	81	152
<i>H. nidi</i> Michael	40	383	50	473
<i>H. nidiformis</i> Bregetova	17	211	5	233
<i>H. ambulans</i> (Thorell)	91	790	81	962
<i>Myonyssus ingricus</i> Bregetova	2	68	0	70
<i>Hirstionyssus isabellinus</i> (Oudemans)	516	3,366	380	4,262
<i>H. talpae</i> Zenskaya	8	627	2	637
<i>Laelaps clethrionomydis</i> Lange	237	1,936	94	2,267
<i>L. hilaris</i> C.L. Koch	168	4,565	133	4,866
<i>Hyperlaelaps microti</i> (Ewing)	259	945	123	1,327

The percentage of the parasite population found on each host species was calculated and used as a measurement of the host preference. When illustrating the numerical distribution of each parasite species on the host species, the abscissa was divided into sections proportional to the percentage of the host species in the region. Thus, the area under the bars became proportional to the percentage distribution of the parasite and the height of the bars indicated the "importance" of the host species to the parasite in the region.

For each ectoparasite species, the hosts were classified according to the number of parasites carried. It was necessary to use a variable class width to get a sufficient number of hosts in each class, since the parasite frequency distribution was often highly clumped. The class width was chosen so that the expected value of each distribution class was ≥ 5 . The distributions were compared with one another by means of $(r \times k) \chi^2$ -test. A significance level of 5 % was accepted. This method was preferred

to calculate the arithmetic means and comparing them with a Z-test, or the non-parametric Mann-Whitney U-test, because the prevalence was mostly very low. A low prevalence implies that non-infested but potential hosts strongly contribute to the arithmetic mean.

Results

There were significant correlations between observed and expected prevalence in the laelapin mites and two of the three lice species (Tab. II:3). For the third louse species, none of the correlation coefficients were significant. Among the haemogamasin mites three out of eight correlation coefficients were statistically significant. In the Hirstionyssinae mites one species had significant and one non-significant correlation coefficients.

Two of the five investigated Haemogamasinae species were particular in their host preference, viz. *Eulaelaps stabularis* by being pronouncedly catholic, and *Haemogamasus horridus* by preferring shrews (Fig. II:1). *Haemogamasus nidi* and *H. ambulans* occurred on voles in the four regions, but were to a small extent found on shrews. *H. nidiformis* was found on voles in the three easternmost regions, and on shrews only in region II. There were also differences in host preferences from one region to another. *H. nidi* was mostly found on *Clethrionomys rufocanus* and *Microtus oeconomus* in the east. In region II, *M. agrestis* was equally important, while the latter species dominated as host in region I.

Hirstionyssus isabellinus and *H. talpae* differed in host preference (Fig. II:2). *H. isabellinus* was associated with voles and mostly found on *C. rufocanus* in regions II and III and on *M. agrestis* in regions I and IV. The shrew *Sorex araneus* was the main host for *H. talpae* in all regions.

Of the six species in the Laelapinae-Anoplura group three were found on species of *Clethrionomys*, viz. *Laelaps clethrionomydis* and *Hoplopleura edentula* on *C. rufocanus* and *Polyplax borealis* on *C. rutilus* (Fig. II:3). *Laelaps hilaris*, *Hyperlaelaps microti* and *Hoplopleura acanthopus* were *Microtus* parasites and mostly found on *M. oeconomus* (Fig. II:4), though *H. acanthopus* was most often found on *M. agrestis* in region II. *M. oeconomus* was missing from region I and *Laelaps hilaris* and *Hyperlaelaps microti* were exclusively found on *M. agrestis* in this region. 78.8 % of all *Hoplopleura acanthopus* in region II were found on *M. agrestis* compared with 85.7 % on *M. oeconomus* in

Table II:3. Correlation coefficients between observed and expected prevalences of Laelapidae mites and lice from northernmost Finland, Norway and Sweden. The total area was subdivided into four regions and the trapping localities into twelve biotopes. * gives the significance level.

Parasites		correlation coefficients	
subfamily	species	region	biotope
ACARI			
Haemogamasinae			
	<i>Eulaelaps stabularis</i>	0.74	0.25
	<i>Haemogamasus nidi</i>	0.78	0.78**
	<i>H. nidiformis</i>	0.86	0.55*
	<i>H. ambulans</i>	0.93*	0.48
Hirstionyssinae			
	<i>Hirstionyssus isabellinus</i>	0.99**	0.55*
	<i>H. talpae</i>	-0.18	0.44
Laelapinae			
	<i>Laelaps clethrionomydis</i>	0.95**	0.98***
	<i>L. hilaris</i>	0.96**	0.98***
	<i>Hyperlaelaps microti</i>	0.98**	0.97***
ANOPLURA			
Hoplopleurinae			
	<i>Hoplopleura acanthopus</i>	-0.20	0.04
	<i>H. edentula</i>	0.94*	0.54*
Polyplacinae			
	<i>Polyplax borealis</i>	0.99***	0.87***

Figs II:1-4. The numerical distribution of ectoparasites in percent on host species in four regions in northernmost Finland, Norway and Sweden. The region axes are divided into sections proportional to the frequency of the host species in each region. The area under each bar is proportional to the percentage of the parasite population found on each host species. The host species are: 1. *Sorex araneus*, 2. *S. caecutiens*, 3. *S. minutus*, 4. *Neomys fodiens*, 5. *Clethrionomys glareolus*, 6. *C. rutilus*, 7. *C. rufocanus*, 8. *Microtus agrestis*, 9. *M. oeconomus*, 10. *Mus musculus*.

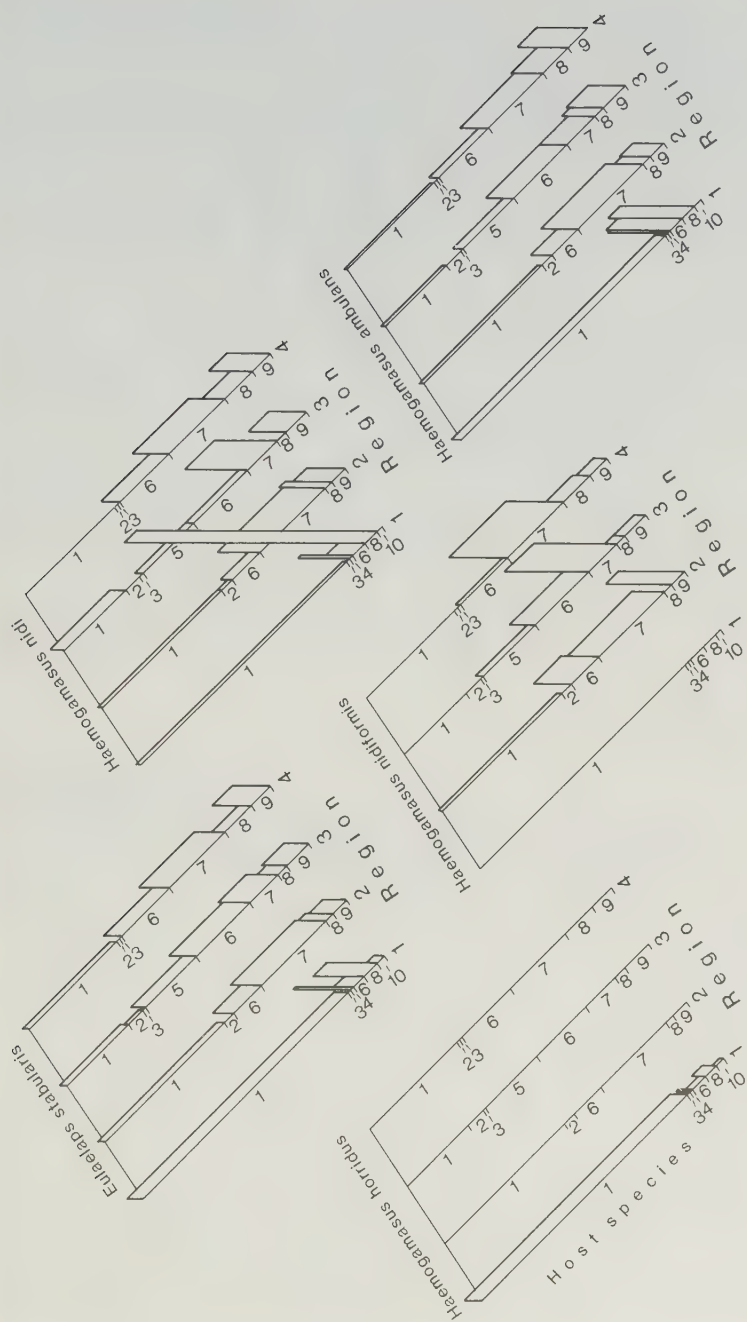


Figure II:1. Numerical distribution of Haemogamasinae mites.

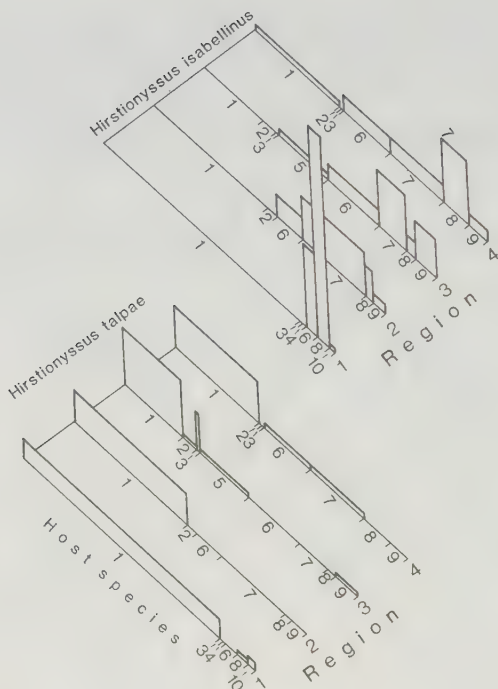


Figure II:2. Numerical distribution of Hirstionyssinae mites.

region III. There was no such switch of host between regions among the *Clethrionomys* specialists (Fig. II:3). *Laelaps clethrionomydis* and *Hoplopleura edentula* were both found on *C. rufocanus* and infrequently on *C. rutilus* and *C. glareolus* when these were present. None of these two ectoparasites were found in region I, where *C. rufocanus* was absent. Neither was the third *Clethrionomys* specialist, *Polyplax borealis*, found in region I, in spite of the presence of its host *C. rutilus*.

Both short- and long-tailed frequency distribution patterns were recognized (vide Figs II: 5-8). All four haemogamasin mites exhibited short-tailed frequency distributions with terminal classes with > 1 or > 2 parasites per host (Fig. II:5). Also *Hirstionyssus talpae* (Fig. II:6) and *Hyperlaelaps microti* (Fig. II:8) had short-tailed frequency distributions. Other distributions were all long-tailed with terminal classes of > 6 (*Polyplax borealis*), > 10 (*Hirstionyssus isabellinus*, *Laelaps clethrionomydis*, *L. hilaris* and *Hoplopleura acanthopus*) or even > 50 (*Hoplopleura edentula*).

Regional differences in frequency distribution pattern on hosts were found in most species. The frequency distribution of *Eulaelaps stabularis* in region I differed from that in the regions II, III and IV. The distribution of *Haemogamasus nidi* was significantly different between the regions I + III, II and IV (Fig. II:5). The frequency distribution patterns of the two *Hirstionyssus* species in region IV differed significantly from those in the other regions. Furthermore, the distribution of *Hirstionyssus isabellinus* in region I was significantly different from that of regions II and IV (Fig. II:6). There was no difference in the distribution of *Laelaps clethrionomydis* between regions III and IV, while that of region II was different (Fig. II:7). Also the frequency distribution pattern of *Hoplopleura edentula* was statistically different in region II from that of regions III and IV. For the third *Clethrionomys* specialist, *Polyplax borealis*, all three regions (II, III and IV) presented significantly different distributional patterns. For the two *Microtus* specialist mites, *Laelaps hilaris* and *Hyperlaelaps microti*, all observed regional differences were significant. The frequency distribution pattern of *Hoplopleura acanthopus* was the same in the two regions (II and III) where this species occurred (Fig. II:8).

The four haemogamasin mites were all less prevalent than expected in localities close to buildings and refuse tips. They were also less prevalent on *Empetrum* - *Betula nana* heaths, mires and mire-edges. They were more prevalent than expected on poor birch localities. On other localities *Haemogamasus nidi* was often in a reversed relationship to the other Haemogamasinae species. This was the case in e.g. rich birch forest, poor pine forest and mixed swampy forest. *Hirstionyssus isabellinus* was often found in expected prevalences in the investigated biotopes. *Hirstionyssus talpae* was more prevalent than expected in open localities and in deciduous forests, except hay meadow and rich birch forest. Laelapin mites were most often found in expected prevalences and so were two of the three lice species. The one exception was *Hoplopleura acanthopus*. This louse was found almost exclusively in three biotopes, viz. poor and rich birch forest and hay meadow. In spite of high expectancy it was not found in swampy spruce forests, willow shrub lands, mire edges and mires, although these biotopes were well represented in the two regions (II and III) where the louse species was found (Tab. II:1). Neither were any lice found in the *Empetrum* - *Betula nana* heath and only in low prevalence in localities close to buildings and refuse tips.

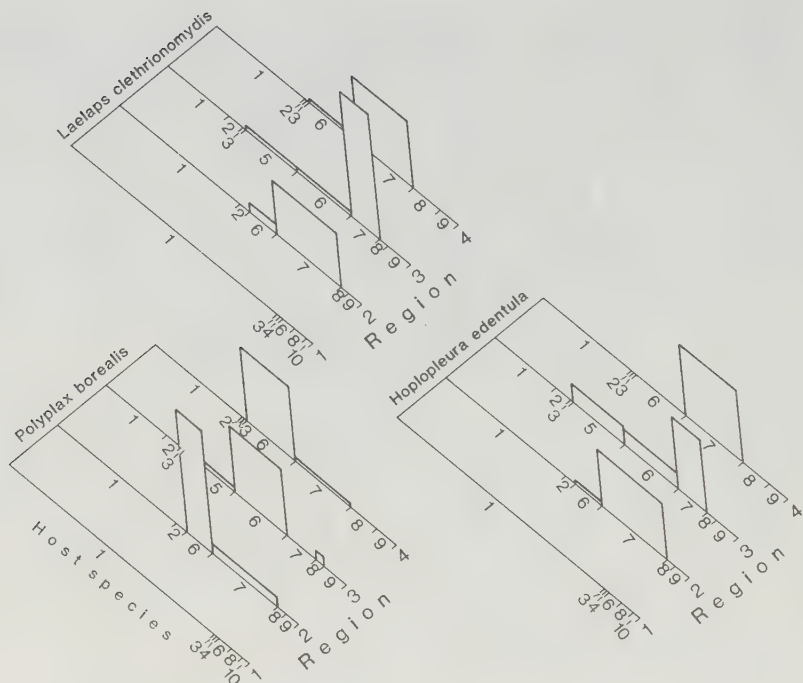


Figure II:3. Numerical distribution of Specialists on *Clethrionomys* spp

Discussion

Part-time and full-time ectoparasites differ in their use of the host's natural environment. For the full-time parasites, it is a pure transition habitat (Stenseth 1983), but is used for reproduction by the part-time parasites. Janion (1983) called it the "secondary habitat"; a term that might be used without implicit ranking.

When the expected prevalence of a parasite population was calculated, the host species frequency was considered (cf. Methods). A high correlation coefficient between expected and observed prevalences therefore indicates a low influence of the secondary environment on the parasite popula-

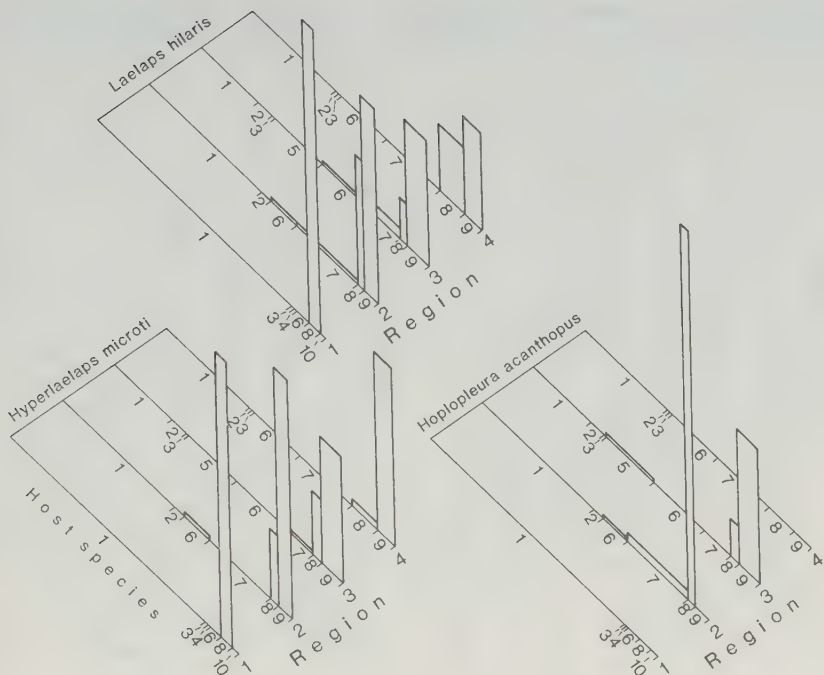


Figure II:4. Numerical distribution of Specialists on **Microtus** spp.

tion. Such a high correlation coefficient was postulated in the Introduction for laelapin mites and low correlation coefficients for haemogamasin mites. The hypothesis was not falsified when the effect of regions and biotopes on the prevalence was tested. The effect of different biotopes was slightly more pronounced (lower correlation coefficients in Tab. II:3) than that of the regions, but both were lower for Haemogamasinae than for Laelapinae and Anoplura. The conceivable mechanism behind such an influence is probably found in the transmission (immigration-emigration) and the reproductive rates of the parasites (Anderson 1976, Anderson and May 1978). Haemogamasin mites are mainly nest inhabitants (Mrčiak et al. 1966). Generally, they enter the hosts in the nests. Laelapin mites are host dwelling and are seldom met with off the host. The main way of transfer for the laelapin mites is therefore by direct contact between host animals, e.g. when suckling or mating. Lundqvist (paper I) put Anoplura and Laelapinae into the same life-trait group and they could hence be expected to be only slightly influenced by the secondary environment. This was not contradicted by our results - except for the louse **Hoplopleura acanthopus**.

Figures II:5-8. Frequency distribution of ectoparasites on hosts in four regions in northernmost Finland, Norway and Sweden. Hosts are classified according to their ectoparasitic burden.



Figure II:5. Frequency distribution of Haemogamasinae mites.

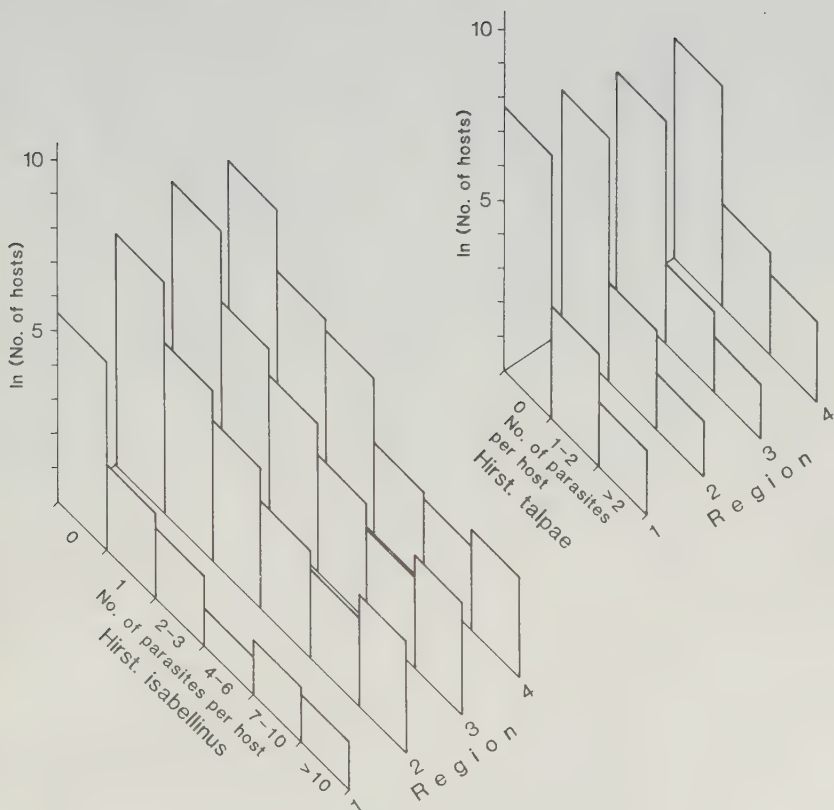


Figure II:6. Frequency distribution of Hirstionyssinae mites.

The immigration rate of a part-time parasite can be increased by increasing the number of possible host species (cf. paper I). The transmission as well as the reproduction rates are reflected in the frequency distribution pattern of the parasite on the hosts (Randolf 1975, Anderson 1976). The haemogamasin mites were more catholic and opportunistic in their host selection. Switching from one host species to another was observed, leading to an infestation of the host species in proportion to their frequency in the region. Laelapin mites had a more restricted host selection and switching between host species was less common. The Anoplura species were similar to the Laelapinae in these respects.

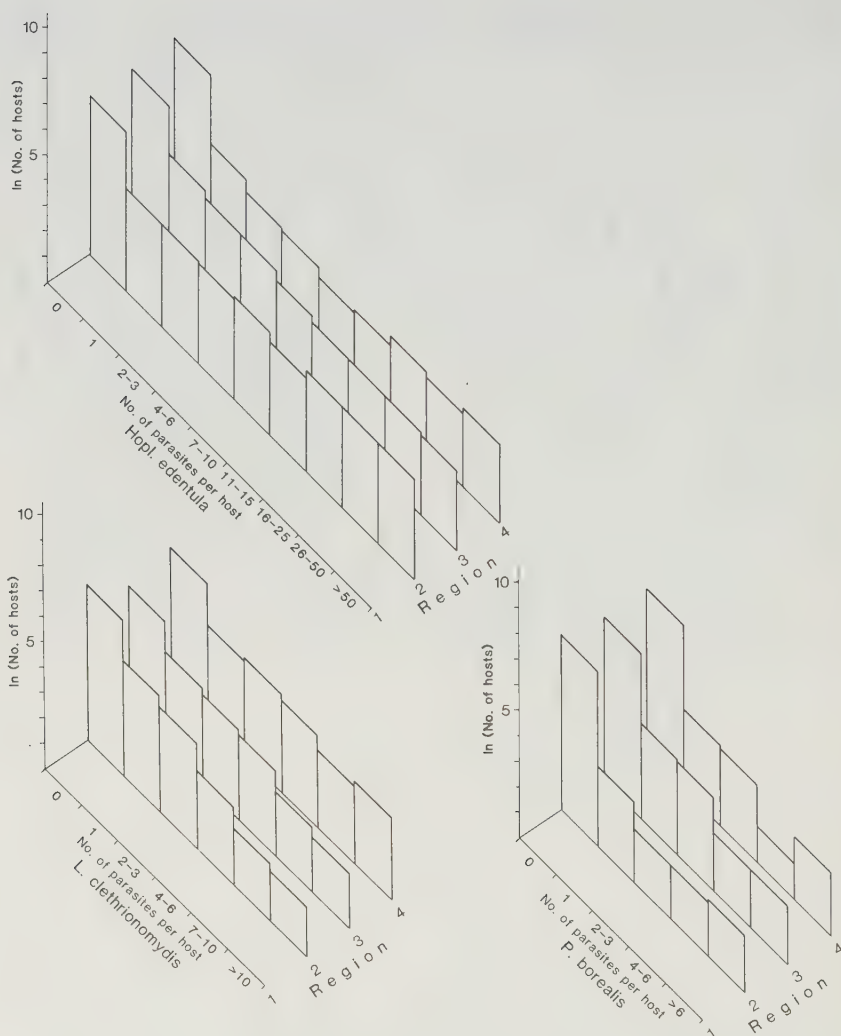


Figure II:7. Frequency distribution of Specialists on *Clethrionomys* spp

All haemogamasin mites had short-tailed frequency distributions, and the laelapin mites, except *Hyperlaelaps microti*, and the Anoplura had long-tailed. There were differences in the frequency distribution patterns between regions. The reproduction of both Haemogamasinae and Laelapinae

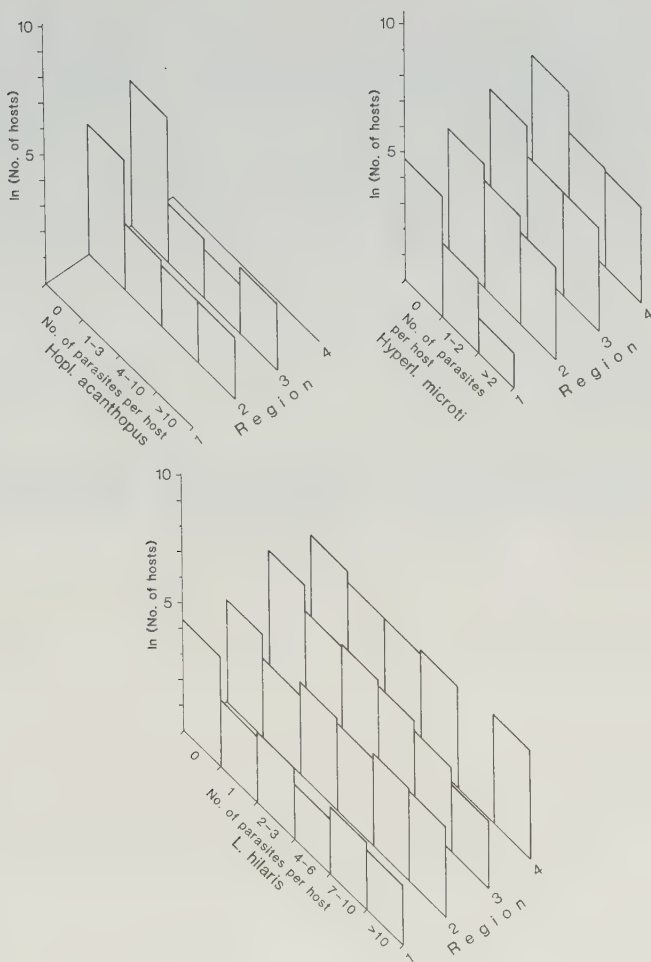


Figure II:8. Frequency distribution of Specialists on *Microtus* spp.

mites were seasonal in Central Sweden (Edler 1972) and South Sweden (Edler 1973). Artz (1975) showed that there is a seasonal incidence of the lice *Hoplopleura acanthopus* and *H. edentula* in northern Germany. We interpret observed regional differences as originating from different seasonality due to climatic conditions in the regions.

The louse *Hoplopleura acanthopus* did not follow the Anoplura scheme as concerns expected prevalence. The species was found only in regions II and III, while its main hosts, *Microtus* spp. occurred in all regions. A parasite distribution restricted to a part of the host's range makes the expected prevalence low. This property of the method used made the differences great between observed and expected prevalences. But it does not explain why the louse was restricted to certain inland regions and biotopes.

Acknowledgement

A special thank is due to Eva Waldemarsson-Jensén, Department of Plant Ecology, Lund, who helped us with the designation of the biotopes.

THE ESTIVAL ECTOPARASITIC BURDEN OF SIX SMALL MAMMAL SPECIES
IN NORTHERNMOST FENNOSCANDIA

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Abstract

The total estival ectoparasitic burden of six small mammal species (*Sorex araneus*, *Clethrionomys glareolus*, *C. rutilus*, *C. rufocanus*, *Microtus agrestis* and *M. oeconomus*) was investigated as regards prevalence, frequency distribution and joint occurrences of species. The mammals were collected during peak density years. The frequency distribution of the total ectoparasitic burden could be described as negative binomial on *C. glareolus*, *M. agrestis* and *M. oeconomus* but not on *S. araneus*, *C. rutilus* and *C. rufocanus*. The fit to Poisson distribution was bad in all host species. Of *S. araneus* 51 % had no ectoparasites, and only 0.6 % (10 specimens) had more than 16. Of the voles, 4 - 27 % had no ectoparasites and the number of parasites on the median of each host species varied between 1 - 9 and the number of species between 1 - 2. On heavily infested voles one ectoparasitic species, usually a louse, dominated and made up 41-100 % of the ectoparasites. The dominating louse species was *Hoplopleura edentula* on *Clethrionomys* spp. and *H. acanthopus* on *Microtus agrestis*. There was a significant, positive correlation between the number of ectoparasitic species and specimens on all host species. Pairs of ectoparasitic species occurring together more or less often than expected, were found on all host species, but seemed to form rather loose connections. Differences were noted in the overall infestation between the sexes of *M. agrestis* but not among *S. araneus* and *C. glareolus*.

Introduction

There are several reports on ectoparasitic species displaying negative binomial distributions on their small mammal hosts (Cf. Crofton 1971, Randolph 1975, Robbins and Faulkenberry 1982). In these studies the zero class, i.e. potential but non-infested hosts dominates; but attention was most often paid to only one ectoparasitic species at a time. The situation prompted us to ask the following questions: "Is a host individual that lacks one particular ectoparasitic species instead infested by another species? Do some host individuals attract more ectoparasites than others, or are all equally infested but by interchangeable species?"

There are many reasons for an overdispersed distribution in parasites (Crofton 1971). If, for one reason or another, one host individual is attracting many ectoparasitic species, then we would expect a covariation of the number of species and the number of specimens on each host.

The existence of interacting or associated pairs of ectoparasitic species may influence the number of ectoparasites on each host. Therefore, we looked for the presence of such pairs.

Material

Six small mammal species were investigated, viz. *Sorex araneus* L., *Clethrionomys glareolus* (Schreber), *C. rutilus* (Pallas), *C. rufocanus* (Sundevall), *Microtus agrestis* (L.) and *M. oeconomus* (Pallas). (c.f. Thesis, Tab. 1). In this investigation we used only hosts from density peak years, as a material collected under uniform conditions was desirable.

Methods

The number of ectoparasites was listed for each host and used as a basis for classifying the hosts. Since most hosts had only a few ectoparasites, while some had rather large numbers, it was necessary to use varying class intervals. The observed distributions were compared with negative binomial and Poisson distributions. The best fits to these theoretical distributions were calculated according to the means and the exponent k for negative binomial and to the means for the Poisson distributions.

The number of ectoparasitic species was plotted against the total number of specimens on each host and the product-moment correlation coefficient was calculated for y_1 -values ≥ 3 . Small y_1 's were omitted, since there is a strong relation between the number of specimens and the possible number of species (one specimen can be of only one species).

One way to study pairs of species occurring together is to arrange a 2×2 contingency table, where presence and absence of each species in the pair are denoted in the cells (Pielou 1977). Another method is to compare the parasite frequency distributions at sympatry and allopatry (Engen 1985). Lundqvist and Stenseth (paper V) suggested that the two methods in fact measure different phenomena and recommended a simultaneous use of both. Here we have used Morisita's index (1959) for frequency data, and a χ^2 -test (Southwood 1978) or Fisher's exact probability test (Sokal and Rohlf 1969) for presence-absence data. If any of the cell frequency values of the contingency table was < 5 we used Fisher's test, otherwise the χ^2 -test. Fisher's test was calculated as a one-tailed test. To make it two-tailed we used a significance level of $\alpha/2 = 0.025$.

The presence of two ectoparasitic species on the same host is called a joint occurrence. The number of joint occurrences of two species can be more, or less, numerous than expected by chance. This is tested from pre-

sence-absence data. If the two species influence each others' distribution at sympatry they will be positively, or negatively, correlated as measured by Morisita's index. The two species make up a pair if their joint occurrences are more, or less, numerous than expected and/or they are positively or negatively correlated.

The frequency distribution of the total ectoparasitic burden of different host categories as regards sex and reproductive status was compared with each other by means of $(2 \times k) \chi^2$ -tests. This was done for three host species, viz. *Sorex araneus*, *Clethrionomys glareolus* and *Microtus agrestis*.

Results

The numbers of ectoparasitic species on the six host species were three Anoplura, fourteen Siphonaptera, fifteen mesostigmatic mites and one ixodid tick species (Tab. III:1).

The frequency distribution of the total ectoparasitic burden was negative binomial on *Clethrionomys glareolus*, *Microtus agrestis* and *M. oeconomus* (Fig. III:1). χ^2 -test showed that it was not negative binomial on *Sorex araneus*, *Clethrionomys rutilus* and *C. rufocanus*. The fit of the observed frequency distribution to Poisson distribution was in all cases very bad.

Sorex araneus was the least infested host species (Fig. III:1). The median *S. araneus* had no ectoparasites. Only 10 specimens, out of 1,633 (0.6 %) had more than 16 ectoparasites. The second lowest infested host species were *Clethrionomys rutilus* and *C. glareolus* whose medians had 1 species and 2 and 3 specimens respectively (Figs III:1-2). *C. rufocanus*, *Microtus agrestis* and *M. oeconomus* formed a third group the medians of which had 2 ectoparasitic species and 8, 8 and 9 specimens, respectively.

On all voles infested by more than 60 specimens, one ectoparasitic species most often predominated (Tab. III:2). On most voles (38 out of 43) this dominating species was a louse, on the remaining voles it was a mite. Except one specimen, all *Clethrionomys* voles with more than 60 ectoparasitic specimens were infested by *Hoplopleura edentula*. *Hoplopleura acanthopus* was present on four, out of five, *Microtus agrestis*, but on none of the two *M. oeconomus*.

The number of ectoparasitic species was on all host species positively correlated with the number of specimens (Figs III:3-8). The correlation

Table III:1. Ectoparasitic species and number of each species found on six host species during host peak density years in three regions of northernmost Finland, Norway and Sweden.	Sorex	Clethrionomys		Microtus		Sum
	g l a r a n e u s	q l a r e o l s	r u r t i l s	r u o n s s	o e c s m u s	
Lice						
<i>Hoplopleura acanthopus</i> (Burmeister)	53	18	13	152	826	359 1,421
<i>H. edentula</i> Fahrenholz	9	2,398	2,681	20,878	54	17 26,037
<i>Polyplax borealis</i> Ferris	0	21	483	27	7	0 538
Fleas						
<i>Hystrichopsylla o. orientalis</i> Smit	258	0	117	25	28	1 429
<i>Ctenophthalmus a. agyrtes</i> (Heller)	13	0	8	0	24	0 45
<i>C. u. uncinatus</i> (Wagner)	28	32	46	54	17	0 177
<i>Paleopsylla soricis</i> s.l. (Dale)	2,600	13	48	22	28	15 2,726
<i>Corrodopsylla birulai</i> (Ioff)	345	8	11	24	2	8 398
<i>Catallagia dackenoi</i> Ioff	0	0	1	0	0	0 1
<i>Rhadinopsylla integella</i> Jordan & Rothschild	3	23	3	12	2	9 52
<i>Ceratophyllus</i> sp.	0	0	2	0	0	0 2
<i>Megabothris calcarifer</i> (Wagner)	3	1	10	6	30	59 109
<i>M. rectangulatus</i> (Wahlgren)	20	63	309	454	154	114 1,114
<i>Amalaraeus penicilliger pedias</i> (Rothschild)	27	264	663	673	100	73 1,800
<i>Amphipsylla s. sibirica</i> (Wagner)	11	48	73	142	74	184 532
<i>Peromyscopsylla silvatica</i> (Meinert)	41	49	507	117	48	65 828
<i>P. b. bidentata</i> (Kolenati)	0	3	1	7	15	52 78
Mites						
<i>Eulaelaps stabularis</i> (C.L.Koch)	84	21	64	100	22	30 321
<i>Haemogamasus horridus</i> Michael	138	0	5	0	6	0 149
<i>H. nidi</i> Michael	35	2	22	168	68	33 328
<i>H. nidiformis</i> Bregetova	5	7	42	85	2	17 158
<i>H. liponyssoides</i> Ewing	41	3	1	1	0	2 48
<i>H. hirsutus</i> Berlese	1	0	0	0	0	0 1
<i>H. ambulans</i> (Thorell)	94	50	188	271	64	112 779
<i>Haemogamasus</i> sp.	0	0	0	1	0	0 1
<i>Myonyssus ingricus</i> Bregetova	55	0	0	0	0	0 55
<i>Hirstionyssus isabellinus</i> (Dudemans)	33	111	616	1,755	300	402 3,217
<i>H. talpae</i> Zenskaya	508	5	4	4	1	3 525
<i>H. tetricus</i> Mrciak	0	0	8	5	0	0 13
<i>Iaelaps clethrionomydis</i> Lange	4	12	64	1,016	1	6 1,103
<i>I. hilaris</i> C.L. Koch	10	10	46	108	799	1,682 2,655
<i>Hyperlaelaps microti</i> (Ewing)	11	3	10	21	177	693 915
<i>Ixodes trianguliceps</i> Birula	1,486	89	355	16	145	13 2,104
Sum:	5,916	3,254	6,401	26,144	2,994	3,949 48,658

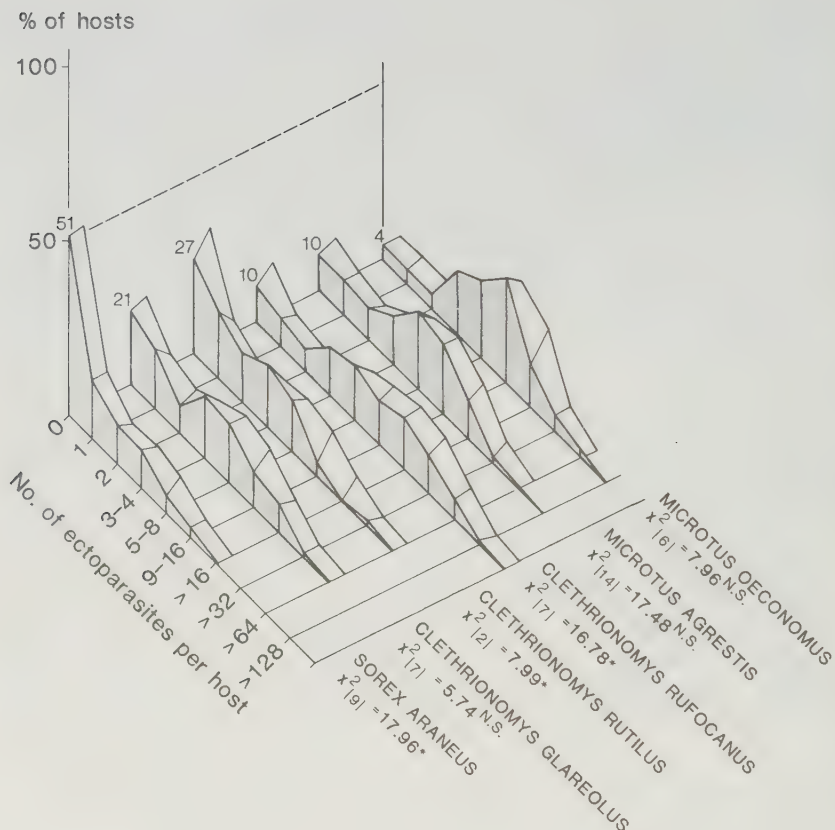


Figure III:1. Frequency distribution of the total estival burden of ectoparasites on six small mammal species in northernmost Finland, Norway and Sweden during peak density years. Observed frequencies are shaded. Expected frequencies are given from χ^2 -tests.

coefficients were statistically significant at 1 % or 0.1 % level tested by two-tailed t-tests. The positive correlation means that a significant proportion of the hosts with more than $\bar{y}_2$ specimens also had more than $\bar{y}_1$ species.

Joint occurrences of ectoparasitic species on *Sorex araneus* were few and the number of correlated species was low (Tabs III:3-4). The fleas dominated among the ectoparasites in both regions I and II. In region I

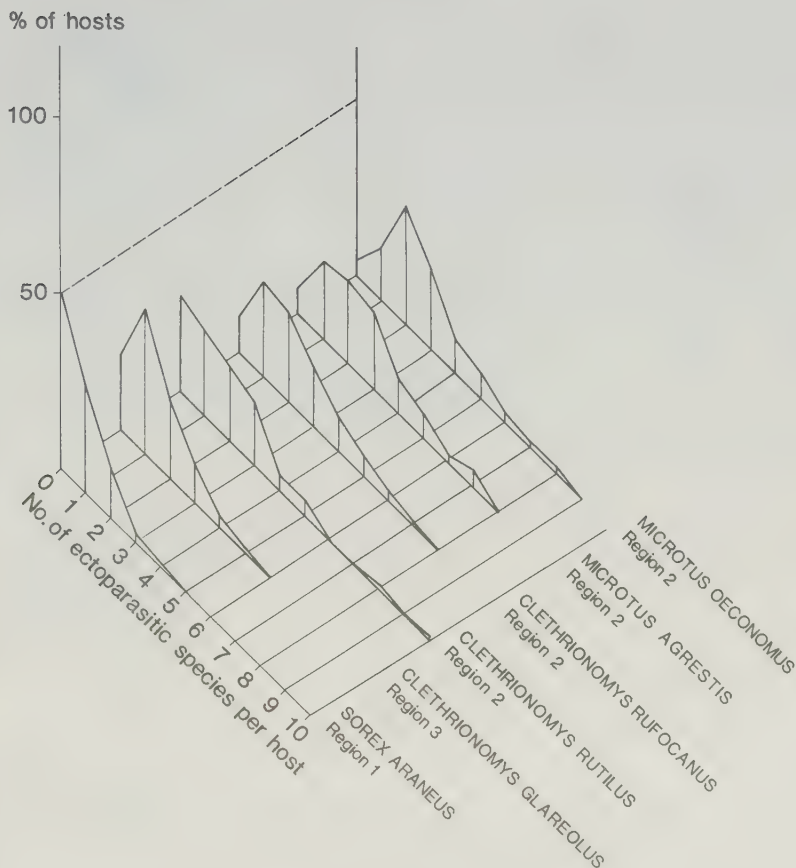


Figure III:2. Frequency distributions of ectoparasitic species found simultaneously on a selection of six small mammal species in northernmost Finland, Norway and Sweden during peak density years.

S. araneus was the dominating host species and consequently most of the fleas were shrew fleas. In region II voles were abundant which was reflected in vole fleas (viz. *Megabothris rectangulatus*, *Amalaraeus penicilliger* and *Peromyscopsylla silvatica*) accidentally occurring on the shrews. None of the pairs from region I was found in region II (Tabs III:3-4).

Table III:2. Dominating ectoparasitic species on hosts with more than 60 ectoparasitic specimens.

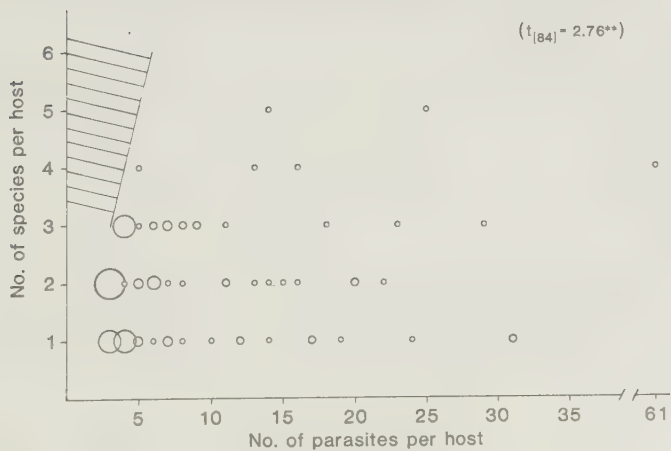
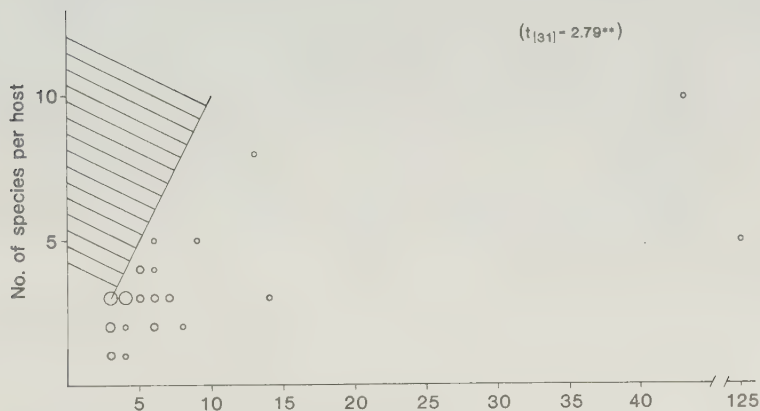
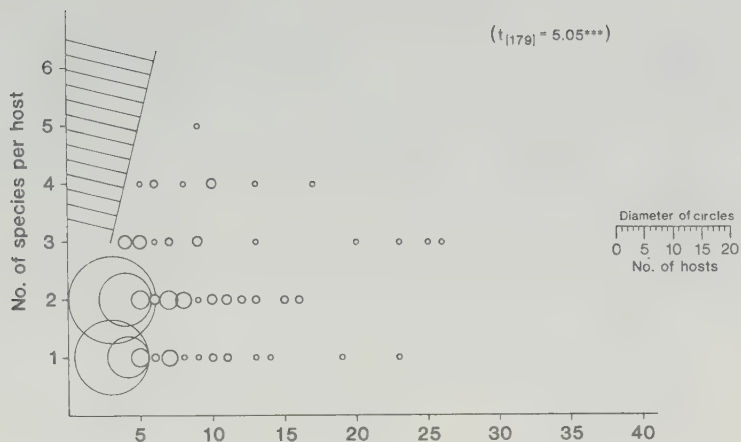
Host species	No. of hosts	Dominating ectoparasitic species	The dominance (% of total) of pre-dominant species		
			min	-	max
<i>Clethrionomys glareolus</i>	1	<i>Hoplopleura edentula</i>			91.8
<i>C. rutilus</i>	2	<i>H. edentula</i>	85.0		96.0
<i>C. rufocanus</i>	1	<i>Hirstionyssus isabellinus</i>		68.9	
	2	<i>Hoplopleura acanthopus</i>	65.0		86.4
	28	<i>H. edentula</i>	76.9		100
<i>Microtus agrestis</i>	1	<i>Laelaps hilaris</i>		41.1	
	1	<i>Hirstionyssus isabellinus</i>		63.0	
	3	<i>Hoplopleura acanthopus</i>	75.3		94.0
<i>M. oeconomus</i>	2	<i>Laelaps hilaris</i>	81.4		90.6

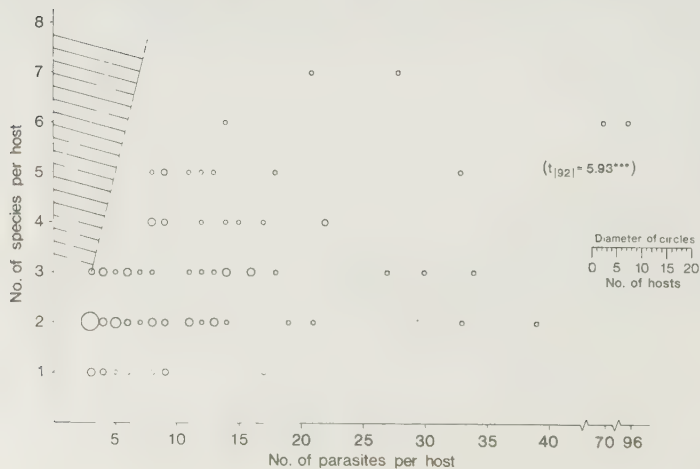
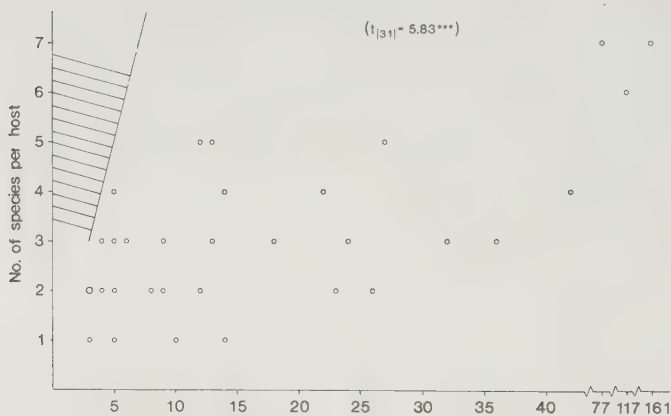
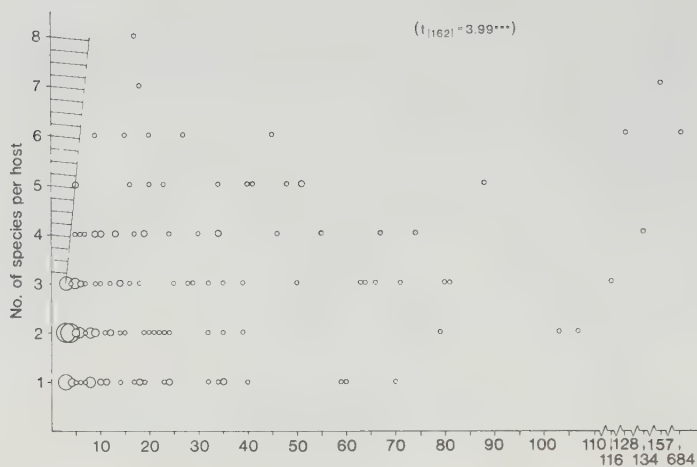
Figures III:3-8. The number of ectoparasitic species plotted against the number of specimens on small mammal species in different regions and years in northernmost Finland, Norway and Sweden during peak density years. The diameter of the circles is proportional to the number of observations. Hatched areas are empty, because there can be no more species than specimens.

III:3. *Sorex araneus*, Lofoten and Vesterålen islands, Norway, 1965.

III:4. *Clethrionomys rutilus*, Abisko and Torneträsk region, Sweden, 1966.

III:5. *C. glareolus*, Vittangi, Sweden and Inari, Finland, 1966.





The number of joint occurrences on *Clethrionomys glareolus* was low (Tab. III:5). However, on *C. rutilus*, with an equally low overall infestation, the number of joint occurrences was high and in several cases higher than expected (Tab. III:6). Joint occurrences were observed several times on *C. rufocanus*, some of them more frequently than expected (Tab. III:7). The mite *Hirstionyssus isabellinus* was positively correlated with the mites *Eulaelaps stabularis* and *Haemogamasus ambulans* on both *Clethrionomys rutilus* and *C. rufocanus*, but the number of joint occurrences was within expectancy. *Haemogamasus ambulans* was found together with *Laelaps clethrionomydis* on both *Clethrionomys rutilus* and *C. rufocanus*. On *C. rutilus* this pair was positively correlated and more frequent than expected, but on *C. rufocanus* the correlation was negative (although not significant) and the number of joint occurrences less than expected. The pair *Amalaraeus penicilliger* and *Megabothris rectangulatus* was the only one found on both *Microtus agrestis* and *M. oeconomus* (Tabs III:8-9).

The frequency distribution pattern of the total ectoparasitic burden was the same in *Sorex araneus* and *Clethrionomys glareolus* as regards sex and reproductive status (Tab. III:10). In *Microtus agrestis*, however, the pattern was different. When comparing the pattern of *C. glareolus* with that of *M. agrestis*, differences were found in subadults but not in adults.

- III:6. *C. rufocanus*, Abisko and Torneträsk region, Sweden, 1966.
 III:7. *Microtus agrestis*, Abisko and Torneträsk region, Sweden, 1966.
 III:8. *M. oeconomus*, Abisko and Torneträsk region, Sweden, 1966.

Table III:3. Number of observed joint occurrences on *Sorex araneus* in region I, 1965.
Number of hosts: 909.

Legend:

No.
R.
F_p / χ^2

H. orientalis

74									
4	C. birulai 9								
32 .156 /8.56	4	P. soricis 254							
2	1	2	C. uncinatus 5						
1	0	5	0	P. silvatica 10					
0	0	9 .112 .005/	0	0	E. stabularis 14				
3	1	12	0	1	0	H. horridus 29			
1	0	4	0	0	0	0	H. ambulans 6		
0	0	3	0	0	0	0	0	H. talpae 7	
24 .176 /4.95	4	77 .144 /15.26	2	5	3	5	4 .776 .022/	1	I. trianguliceps 196

Table III:3-9. Number of observed joint occurrences of ectoparasites on small mammals from northernmost Fennoscandia 1965-70. Numbers under each parasite name give the number of hosts infested by the parasite species. Test statistics are given in cases where $R / > 0.5$ and $No. \geq 3$ or F_p / χ^2 gives a significant level of 5 %. No.: Number of joint occurrences, R: Morisita's index, F_p : Fisher's exact probability test.

Table III:4. Number of observed joint occurrences on *Sorex araneus* in region II, 1965. Number of hosts: 724.

<i>H. orientalis</i>									
5									
1	C. birulai								
	70								
1	.33 .108 /32.69	P. soricis							
		147							
0	2	4	C. unicus						
			7						
0	0	3	0	P. silvatica					
				8					
0	2	4	0	0	A. penicilliger				
					9				
0	1	1	0	0	2	M. rectangulatus			
						8			
0	3 .524 .993/	1	0	0	0	0	E. stabularis		
							9		
0	0	5	0	0	1	1	0	H. ambulans	
								15	
0	2	2	0	0	0	0	0	0	H. isabellinus
									6
0	3 .857 .978/	4 -.868 .925/	0	0	0	0	0	1	0
									H. talpae
									12

Table III:5. Number of observed joint occurrences on *Clethrionomys glareolus* in region III, 1966. Number of hosts: 157.

<i>C. uncinatus</i>									
6									
0	P. silvatica								
	10								
1	2	A. penicilliger							
		50							
1	2	5	M. rectangulatus						
			13						
0	1	4	3	E. stabularis					
				7					
0	0	3	1	2	H. ambulans				
					7				
0	1	6	2	1	1	H. isabellinus			
						17			
4	5	26	4	4 -.682 .606/	4	15 .070 .003/	H. edentula		
						86			

Table III:6. Number of observed joint occurrences on *Clethrionomys rutilus* in region II, 1966. Number of hosts: 84.

C. uncinatus									
6									
0	A. sibirica								
8									
2	3	A. penicilliger							
42									
2	4	9	M. rectangulatus						
13									
2	0	5	4	E. stabularis					
.966 1.100									
.216/ .010/ 7									
2	1	4	2	2	H. ambulans				
.543									
.180/ 5									
5	3	12	9	4	3	H. isabellinus			
.833 -.556 .497 .739 .526									
.007/ .842/ .001/ .099/ .138/ 24									
3	2	11	5	3	5	12	L. clethrionomys		
.451 .246									
.001/ /10.76 20									
2	0	5	1	1	1	6	4	P. borealis	
10									

Table III:7. Number of observed joint occurrences on *Clethrionomys rufocanus* in region II, 1966. Number of hosts: 216.

P. soricens									
6									
0	C. uncinatus								
7									
1	0	A. sibirica							
12									
* 5	4	5	A. penicilliger						
75									
458									
.020/									
3	2	4	25	M. rectangulatus					
				.536					
				/2.72	56				
				.892					
				.960/					
0	1	2	7	6	E. stabularis				
14									
0	1	0	8	4	5	H. nidi			
			.072		.991				
			.010/		1.000/	11			
0	4	1	10	10	8	6	H. ambulans		
					.916	.974			
					/19.71	.001/	30		
					.135				
					.008/				
2	0	5	27	15	4	1	8	H. isabellinus	
						.023	.776	.809	
						/13.51	.848/	/2.85	46
1	2	7	26	19	4	3	13	13	L. clethrionomydis
								.214	
								.016/	

Table III:10. Frequency distributions of the total ectoparasitic burden on host reproductive categories compared to each other by (2 x k) χ^2 -tests. Test statistics are given for each test. There were no subadult *Sorex araneus* in the material but test statistics between juvenile males and females were: $\chi^2_{(4)} = 8.729$ n.s., N = number of hosts.

	Clethrionomys glareolus				Microtus agrestis				Sorex araneus			
	N	χ^2	d.f.	p	N	χ^2	d.f.	p	N	χ^2	d.f.	p
Adult males	28				29				-			
Subad. males	119	6.781	4	n.s.	53	10.814	2	**	0			
Adult females	44				70				-			
Subad. females	85	1.593	5	n.s.	39	11.495	4	*	0			
Adult males	28				29				39			
Adult females	44	2.602	4	n.s.	70	30.867	2	***	36	1.592	2	n.s.
Subad. males	119				53				0			
Subad. females	85	6.390	4	n.s.	39	0.262	2	n.s.	0			
	adult males				adult females				subadult females and males			
C. glareolus	28				44				204			
M. agrestis	29	4.250	2	n.s.	70	6.190	4	n.s.	92	14.744	4	**

Discussion

The proportion of uninfested animals in a host population is sometimes large, and the number of ectoparasites on hosts has a wide range. The tail of such a frequency distribution is long, and localizing a distribution center, like an arithmetic mean or median, becomes less attractive. Sometimes, however, the observed distribution fits a theoretical distribution, e.g. negative binomial. If so, the distribution variables, the mean and the exponent k in the negative binomial, give information on the frequency distribution pattern, and the probability that a host animal harbours 0, 1, 2, 3, ... ectoparasites can easily be calculated (see Lundqvist thesis, section 4, for further discussion).

Sonenshine and Stout (1968) and Nilsson and Lundqvist (1978) suggested that the number of ectoparasites on a host is a result of the hosts vagrancy and the number of encounters between hosts. There are differences in territorial behaviour between reproductive and non-reproductive males and females of *Sorex araneus* (Michielsen 1966), *Clethrionomys glareolus* (Mazurkiewicz 1983) and *Microtus agrestis* (Myllymäki 1977). In *S. araneus* both sexes are territorial and very aggressive. In *C. glareolus* the females are territorial but share common males, and in *M. agrestis* the males have exclusive territories where they keep "harems" of females. There were differences in the frequency distribution patterns of ectoparasites on the reproductive host categories of these three species (Tab. III:10). Many authors (cf. Brinck 1966, Ulmanen and Myllymäki 1971) have pointed out that adult male voles are more infested by fleas than other reproductive categories of hosts. It is, however, not an easy task to correlate the differences in frequency distribution with territorial behaviour of the hosts. To do so we need an experimental set up where we can correlate the occurrence of ectoparasites of different life-traits with e.g. the host's home-range and activity.

Small mammals are profitable resources. They are consumed by numerous predators, and infested by a large variety of parasites. Contacts between the small mammals and their parasites and predators are established under different circumstances. One important difference between parasite encounter and predator encounter is that while the predator actively searches for the prey the parasites most often merely wait to be picked up by a host animal, passing by. Encountering a parasite is therefore highly dependent on what the host is doing, which in turn is dependent, among small mammals, on sex, age, social status etc. The number of parasites on such a

host depends, in addition, on the number of parasites in the area where the host is active. Furthermore, there is probably a heavy random variation. The sum of these properties of the hosts, the parasites and the abiotic factors may lead to a situation of non-equilibrium populations as discussed in detail by Price (1980). Such a situation is indicated by the wide ranges of the number of parasites in most of our host species. Finally, there is probably a great individual variation; some hosts are simply more tasty than others. This is supported by the fact that there was a positive correlation between the numbers of ectoparasitic species and specimens. Alternative explanations could be induced density dependent immune respons, which is a strong control mechanism for internal small mammal parasites (Kennedy 1975), or interspecific exploitation competition (Halvorsen 1976).

While the number of ectoparasitic species on the host was restricted, the situation in the nest is characterized by profusion (Mrciak et al. 1966). But to study nest ectoparasites simply by looking at hosts is, to some degree, to do population studies with too small subsamples. In addition the sampling method is stratified, as the time spent by the parasites on a host differs between species (Peus 1972). In fleas the time spent on a host varies also with the age of the parasite (Marshall 1981, Brinck-Lindroth in ms). The nest parasite population found on the hosts is, therefore, probably biased and reflects only a part of the diversified communities found in nests (Daniel and Holubicková 1972, Lundqvist 1974).

Seasonal variation is not considered in this investigation. Previous studies have shown that there is a change of species as well as prevalence. Many of the flea species are seasonal in appearance (vide Marshall 1981). The same is known for mites (Edler 1973), ticks (Nilsson 1974, 1978) and lice (Artz 1975). Seasonality can be mediated through e.g. temperature and relative humidity (cf. Marshall 1981), reproductive hormonal cycle of the host (Rothschild and Ford 1964) and maybe even of life tactic reason (paper I). Thus, there are a change of ectoparasitic species over the year, but we do not believe that the patterns of the total frequency distribution or the joint occurrences, which are of prime interest here, change much over the season.

IS ECTOPARASITIC INFESTATION IN SMALL MAMMALS A FUNCTION OF HOST SIZE?

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Abstract

The number of ectoparasites on a small mammal host is discussed as a function of host size, i.e. how much of the variation in the number of ectoparasites is explained by variation in host size? The number of ectoparasites was expressed as the number of species and of specimens. Single host species as well as groups of host species and different life-trait groups of ectoparasites were analyzed separately. A significant part of the variation in the number of the ectoparasites was explained by variation in host size when all hosts were pooled together. But when the host species were studied separately most often the relation was bell-shaped, middle-sized hosts being more infested. For full-time ectoparasites a significant part of the variation was explained by host size but there was no such relation for part-time parasites. There are similarities in invasion and extinction/emigration rates between island inhabitants and parasite population dynamics, but there are also important differences in the biology of the invading species.

Introduction

The size of a host may restrict the number of its parasites, as shown by Price (1980) for plants, birds and small mammals. When analyzing the number of ectoparasites on small mammals in relation to host size, Mohr (1961) found a linear regression with more parasites on larger host, while Haitlinger (1983) found a curved relation with more ectoparasites on middle-sized hosts. In this study we analyze the number of ectoparasites on small mammals as an outcome of the host size.

Due to resemblances between islands and any patchy environment, hosts have been compared to islands as concerns the number of species living on them (cf. Dritschilo et al. 1975, Price 1980). Similarities and differences between small mammals as hosts and island bio-geography will be discussed below.

Material and Methods

Host species and their weights used in this study are given in Table IV:1. In addition to the small mammals reported in section two of the thesis, we here include five weasels (*Mustela nivalis*), accidentally collected in the small mammal traps during the field work. Three host species were analyzed separately, viz. *Sorex araneus*, *Clethrionomys rutilus* and *Microtus agrestis* (Tab. IV:2). The analysis of life trait groups is based on the subdivision presented in paper I where haemogamasin mites and Sip-

Table IV:1. Average weights of small mammals in northernmost Fennoscandia 1965-70.

Species	P E A K		Y E A R S		L O W		Y E A R S	
	number	average	weight (g)		number	average	weight (g)	
<i>Sorex minutus</i> L.	2	2.8			7	3.3		
<i>S. caecutiens</i> Laxmann	12	3.5			15	3.4		
<i>S. araneus</i> L.	392	6.9			611	7.0		
<i>Neomys fodiens</i> (Pennant)	-	-			5	10.8		
<i>Clethrionomys glareolus</i> (Schreb.)	-	-			13	18.7		
<i>C. rutilus</i> (Pall.)	69	18.6			127	19.1		
<i>C. rufocanus</i> (Sund.)	279	26.4			57	27.3		
<i>Microtus agrestis</i> (L.)	54	27.7			15	24.0		
<i>Mustela nivalis</i> L.	2	35.3			3	40.7		
<i>Lemmus lemmus</i>	3	37.5			1	26.0		
<i>Microtus oeconomus</i> (Pall.)	15	41.1			14	25.9		

honnaptera represent the part-time parasites, whereas laelapin mites and Anoplura represent the full-time parasites (Tab. IV:2).

The statistical methods were borrowed from island biogeography. Thus, $S = cA^z$ where S is the number of species, A the area of the island and c and z are constants. By transforming into logarithms we get: $\ln(S) = \ln(c) + z \times \ln(A)$, where z becomes the slope in a regression analysis. The significance of the regression was tested by means of an anova, where the explained part of the variation due to the regression line was compared to the error around the regression line. The individual surface area of the hosts was calculated as the weight^{2/3}. The significance of island densities was tested by analyzing small mammal populations from low and peak years separately.

Results

When analyzing the pooled host material, a significant part of the variation among the groups was explained by the regression line (Fig. IV:1). Again, the regression was significant at the analysis of the number of ectoparasitic specimens in relation to host size (Fig. IV:2).

Table IV:2. Number of ectoparasites (n) and infested hosts (N) regions of northernmost Fennoscandia.

Ectoparasitic species	all hosts		all hosts		S. araneus	
	Abisko		all regions		Lofoten	
	peak years		low years		peak years	
	n	N(506)	n	N(568)	n	N(543)
SIPHONAPTERA						
<i>Hystriopsylla o. orientalis</i> Smit	132	78	20	18	118	81
<i>Ctenophthalmus a. agyrtus</i> (Heller)	11	8	0	0	7	7
<i>C. u. uncinatus</i> (Wagner)	22	20	39	28	7	6
<i>Palaeopsylla soricis</i> s.l. (Dale)	760	28	272	102	974	333
<i>Corrodopsylla birulai</i> (Ioff)	61	24	77	145	12	8
<i>Rhadinopsylla integella</i> Jordan & Rothschild	3	3	1	1	0	0
<i>Ceratophyllus l. lunatus</i> Jordan & Rothschild	1	1	0	0	0	0
<i>Megabothris calcarifer</i> (Wagner)	5	5	1	1	0	0
<i>M. rectangulatus</i> (Wahlgren)	124	69	200	119	1	1
<i>Amalarseus penicilliger pedias</i> (Rothschild)	165	77	258	141	3	2
<i>Amphipsylla s. sibirica</i> (Wagner)	35	24	102	68	0	0
<i>Peromyscopsylla b. bidentata</i> (Kolenati)	4	2	3	3	0	0
<i>P. silvatica</i> (Meinert)	104	27	11	8	13	11
ANOPLURA						
<i>Hoplopleura acanthopus</i> (Burmeister)	33	1	550	30	0	0
<i>H. edentula</i> Fahrenholz	780	39	5,584	186	0	0
<i>Polyplax borealis ferris</i>	87	12	30	12	0	0
Acari						
LAELAPIDAE						
Haemogamasinae						
<i>Eulaelaps stabularis</i> (Koch)	41	31	65	47	21	21
<i>Haemogamasus horridus</i> Michael	69	52	0	0	41	36
<i>H. nidi</i> Michael	63	28	98	39	7	5
<i>H. nidiformis</i> Bregetova	17	10	13	6	0	0
<i>H. liponyssoides</i> Ewing	1	1	1	1	0	0
<i>H. ambulans</i> (Thorell)	95	61	128	73	13	13
Hirstionyssinae						
<i>Hirstionyssus isabellinus</i> (Oudemans)	178	48	431	84	1	1
<i>H. talpae</i> Zenskaya	35	17	321	6	34	11
<i>H. tatricus</i> Mrciak	2	1	7	4	0	0
Myonyssinae						
<i>Myonyssus ingricus</i> Bregetova	6	4	3	3	32	20
Laelapinae						
<i>Laelaps clethrionomydis</i> Lange	179	34	196	94	0	0
<i>L. hilaris</i> Koch	147	23	382	57	1	1
<i>Hyperlaelaps microti</i> (Ewing)	44	14	57	21	2	1

<i>S. araneus</i>		<i>C. rutilus</i>		<i>C. rutilus</i>		<i>M. agrestis</i>		<i>M. agrestis</i>	
Lofoten		Abisko		all regions		Vittangi		all regions	
low years		peak years		low years		peak years		low years	
n	N(299)	n	N (50)	n	N (90)	n	N (43)	n	N (14)
53	36	0	0	55	22	0	0	5	5
2	2	0	0	3	3	0	0	6	3
1	1	4	2	4	4	0	0	2	2
625	222	0	0	16	7	0	0	1	1
0	0	0	0	1	1	1	1	0	0
0	0	0	0	0	0	1	1	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	4	4	9	6	0	0
2	2	26	15	42	28	15	12	10	7
5	4	63	33	88	36	15	12	6	5
2	2	4	4	3	3	18	13	10	4
0	0	0	0	0	0	14	6	0	0
12	9	0	0	56	11	6	3	7	3
0	0	0	0	0	0	36	4	0	0
0	0	128	3	15	5	15	2	0	0
0	0	28	11	81	10	3	1	0	0
12	11	8	6	4	4	4	4	0	0
65	48	0	0	2	2	0	0	1	1
6	5	7	3	6	3	0	0	2	2
0	0	3	1	2	2	2	2	0	0
0	0	0	0	0	0	0	0	0	0
26	16	9	6	26	17	25	10	5	5
3	3	50	16	57	21	23	10	1	1
20	11	0	0	0	0	0	0	0	0
0	0	3	2	0	0	0	0	0	0
2	2	0	0	0	0	0	0	0	0
2	2	18	14	10	6	0	0	0	0
0	0	2	1	35	3	58	25	75	5
0	0	0	0	2	1	77	15	9	3

Figures IV:1-6. Number of ectoparasites in relation to the size of small hosts in northernmost Fennoscandia (cf. Fig. I:1). N: number of hosts.

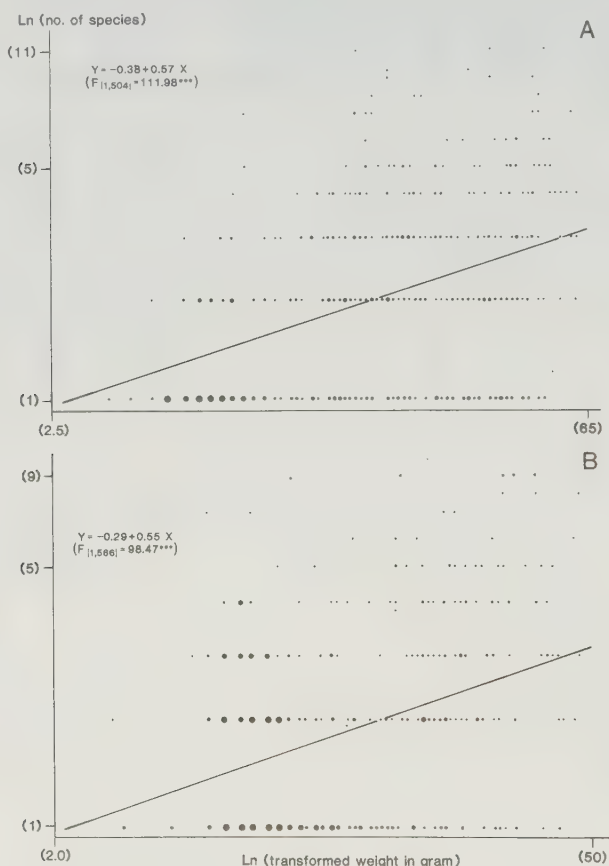


Figure IV:1. Host species pooled, a) Abisko, peak years, N: 506.
b) all regions, low years, N: 568.

Single host species analyzed separately showed no significant, linear regression between the number of ectoparasitic species and host size (Fig. IV:3). Instead, there was a bell-shaped pattern, with middle-sized hosts being most infested. However, the linear regression between the number of specimens on *Sorex araneus* during peak years and the size of the hosts was significant (Fig. IV:4).

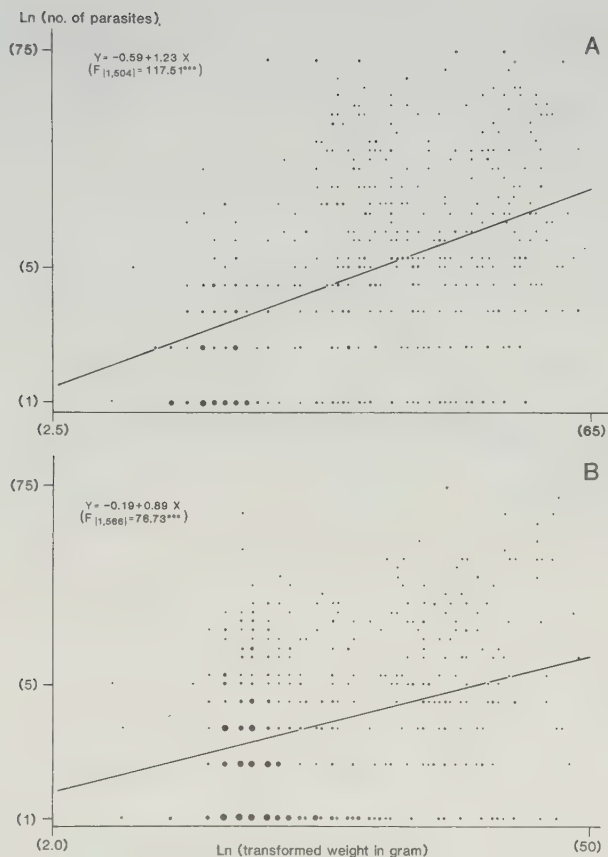


Figure IV:2. Host species pooled, a) Abisko, peak years, N: 506.
b) all regions, low years, N: 568.

The number of part-time ectoparasites was not significantly explained when related to the size of *Clethrionomys rufocanus* hosts (Fig. IV:5), but the regression of full-time ectoparasites was significant at the 5 % level (Fig. IV:6).

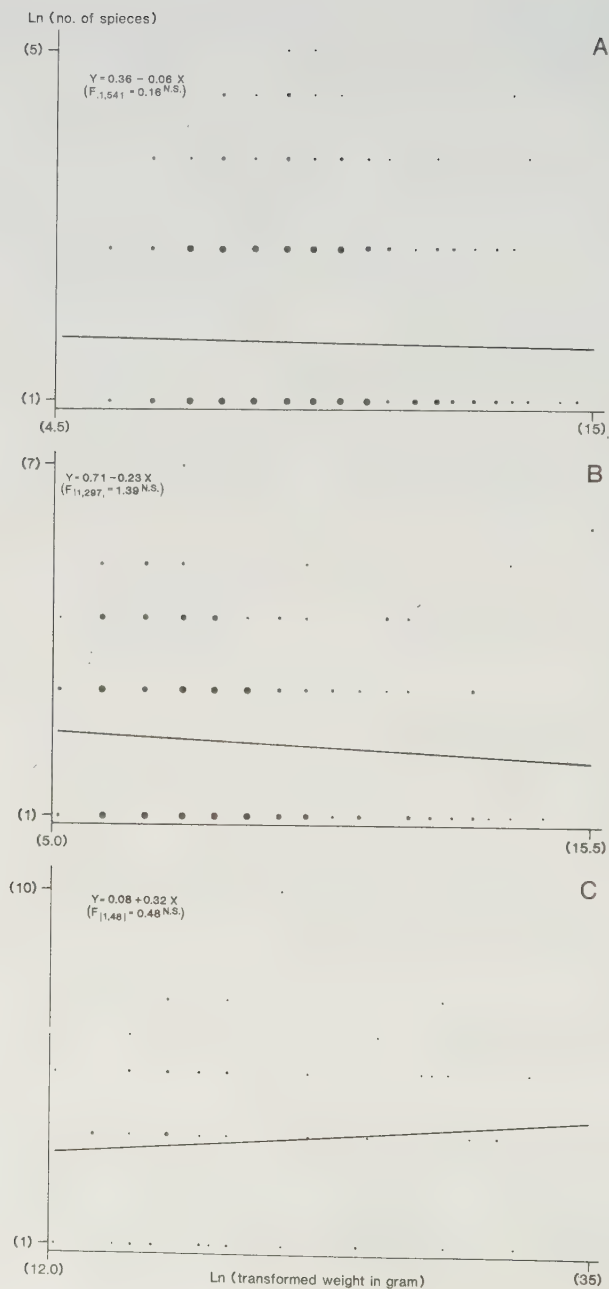


Figure IV.3. Number of species on a) *Sorex araneus*, Lofoten, peak years, N: 543.
 b) *S. araneus*, Lofoten, low years, N: 299.
 c) *Clethrionomys rutilus*, Abisko, peak years, N: 50.

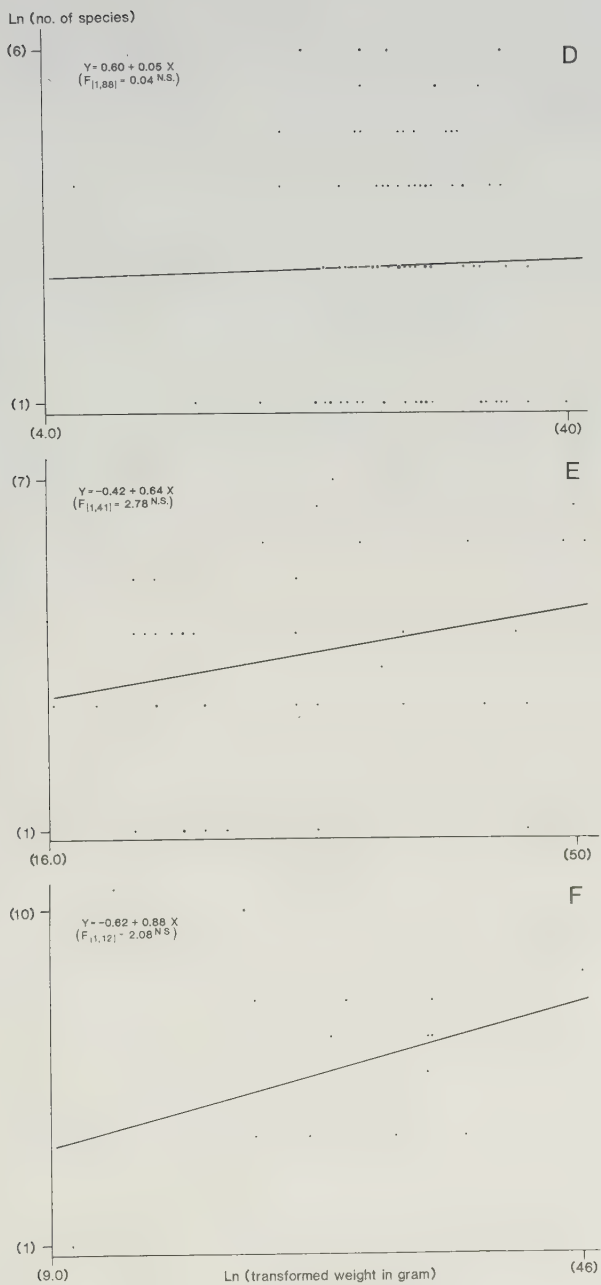


Figure IV:3. Number of species on d) *C. rutilus*, all regions, low years, N: 90.
 e) *Microtus agrestis*, Vittangi, peak years, N: 43.
 f) *M. agrestis*, all regions, low years, N: 14.

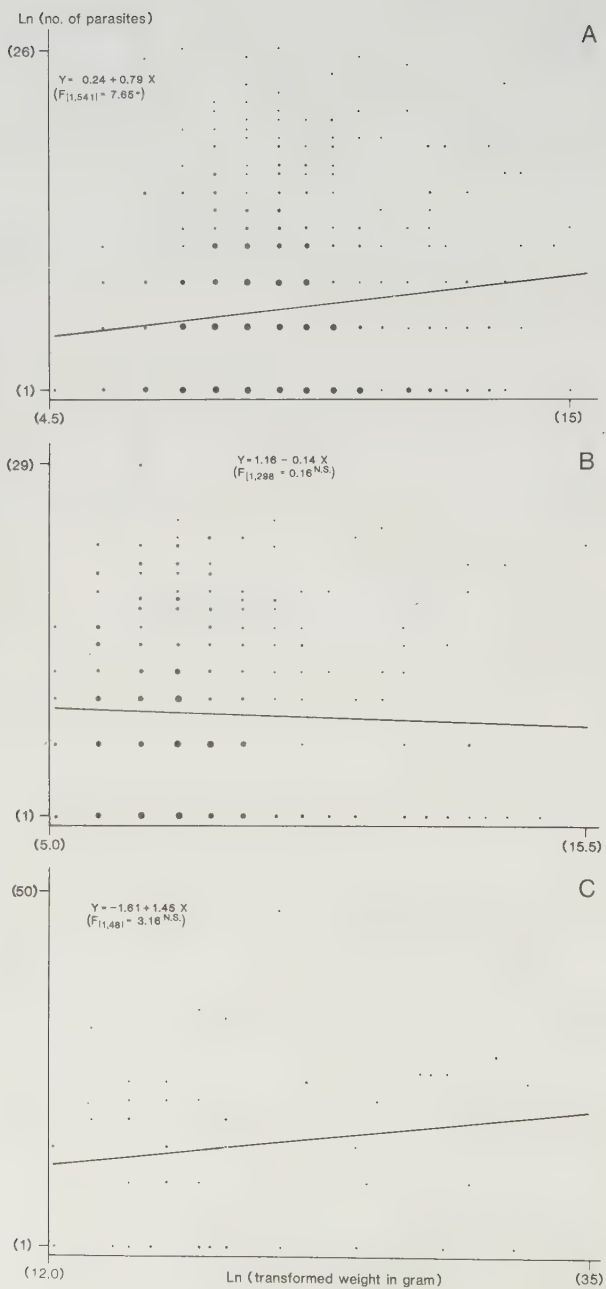


Figure IV:4. Number of ectoparasites on a) *Sorex araneus*, Lofoten, peak years, N: 543.
 b) *S. araneus*, Lofoten, low years, N: 299.
 c) *Clethrionomys rutilus*, Abisko, peak years, N: 50.

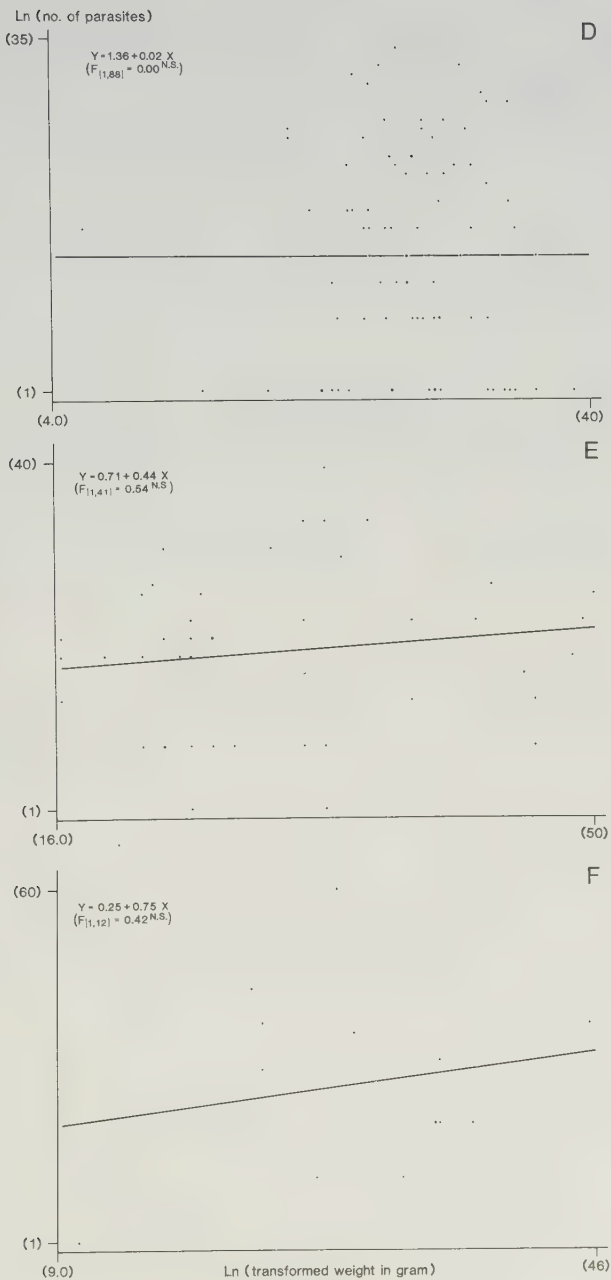


Figure IV:4. Number of ectoparasites on d) *C. rutilus*, Abisko, peak years, N: 90.
 e) *Microtus agrestis*, Vittangi, peak years, N: 43.
 f) *M. agrestis*, all regions, low years, N: 14.

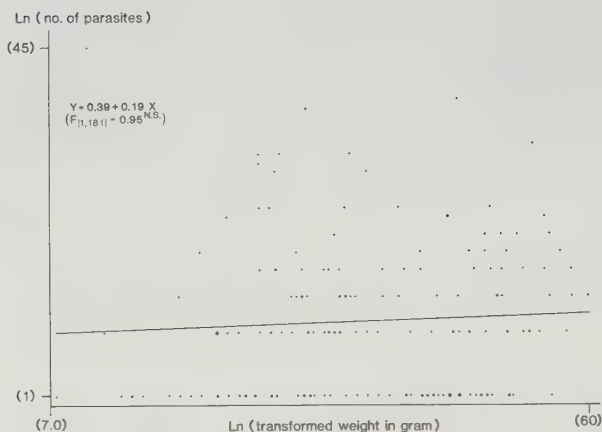


Figure IV:5. Part-time parasites on *Clethrionomys rufocanus*, Abisko, peak years, N: 183.

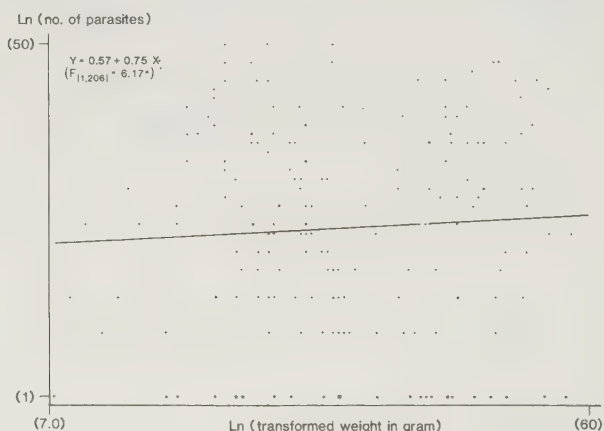


Figure IV:6. Full-time parasites on *C. rufocanus*, Abisko, peak years, N: 208.

Discussion

There are several factors determining the size (or rather the weight) of a small mammal, e.g. sex, age and nutritional status. Other factors are indirectly co-ordinated with weight such as home-range, activity and social status. Most of these factors are more or less important also for the ectoparasites (cf. Marshall 1981), although little is known of how they work in detail.

When the number of ectoparasites was plotted against the size of their small mammal hosts of all species, a significant, positive regression was observed. This is in accordance with Mohr (1961) and Mohr and Stumpf (1964) who studied small mammal species on New Guinea, and Haitlinger (1983) studying ectoparasites on *Clethrionomys glareolus* (Schreb.) in Europe. However, when host animals of one species were studied separately, there was no such simple, linear regression. For one host species the range of the host size on the abscissa is rather narrow and this probably allows for other factors, such as those mentioned above, to mask a possible, linear regression.

When discussing the influence of host age and size on the number of ectoparasite insects, e.g. Hippoboscidae, Mallophaga, Anoplura and Siphonaptera, Marshall (1981:330) concluded that generally there seems to be more ectoparasites on young, and hence small, hosts than on adults. This gives bell-shaped regressions like those found in Figs IV:3-4. Such a pattern can be explained by acquired immunity (Kennedy 1975), Wakelin 1976) or by adults being more efficient at grooming. Malnutrition, which is more likely in small animals than in large, is another factor that seems to make ectoparasite establishment easier, especially low-protein diet and deficiency in vitamins A and the B-complex (Nelson 1984).

According to MacArthur and Wilson (1967) the species density in an island habitat is a dynamic equilibrium at the intersection point between immigration and extinction rates. Similarly, the number of parasites on a host is the result of immigration/emigration and birth/death rates (Anderson 1976). By deductive reasoning large hosts, like large islands, should have more species than small hosts. This was confirmed by observations when the abscissa comprised several host species.

In comparison with studies on other organisms, the z values, the slope in species/area regression, in Fig. IV:1 were very high. In recent publications on bio-geography, the biological meaning of z has been under debate (cf. Abbott 1983). However, large values of z often result from diversified habitats. We might therefore conclude that small mammals act as highly stratified environments. This is in accordance with Nilsson (1981) who subdivided the small mammal body into ten areas and showed that each had its typical ectoparasite species or group of species.

Clumped islands, such as an archipelago, often have higher immigration rates and higher z -values than scattered islands. There were, however, no observed differences in the z values of the ectoparasites between peak density years and low years in the small mammal dynamics.

For full-time ectoparasites the small mammals serve as islands. The parasite species invade the hosts, start to reproduce and stay on their hosts. Part-time ectoparasites, however, include part of the "secondary environment" (paper II) in their optimal habitats. For these species the small mammals are not island habitats but samples from populations which share the same nests and run-ways.

The number of specimens of most ectoparasitic species on one host individual is often low (cf. papers I and II). In such a situation the random arrival or death of one or a few parasite individuals may have a great influence on the composition of the parasite population on the host. This stochastic element of immigration and extinction rates is a further reason why care must be exercised when hosts of ectoparasites are compared with islands (cf. Simberloff 1976).

ASSOCIATION, INTERACTION AND NICHE-OVERLAP

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Abstract

Association between species is defined as a measure of similarity of resource, or habitat, usage. Interaction, on the other hand, is defined as the direct effect (positive or negative) of one species on a sympatric species' specific population growth rate. It is discussed how these concepts of association and interaction are related to niche-overlap.

Both real and simulated data are analyzed on this basis.

Introduction

Imagine two species occurring on islands. They may, for two different reasons, co-occur more or less frequently than expected by chance: 1) they may require more or less similar resources, or 2) they may outcompete or mutually benefit each other. This distinction is only rarely made explicit. Pielou (1977: 203) states, for example, that "if two co-occurring species are affected by the same environmental factors, or if they have some effect, either favourable or unfavourable, on each other, their patterns will not be independent; the species will be associated, either positively or negatively". Then she describes how to measure association but does not distinguish between resource determined co-occurrence, competition and mutualism. Other authors also fail to make the difference clear (cf. Schoener 1983).

The purpose of this paper is to specify the concepts of association and interaction (positive or negative) and to point out some of their essential differences. In addition we compare two methods commonly used for measuring association and interaction by using both real and simulated data.

Association is a widely used term having many different meanings. We suggest that the meaning of "association" is restricted to the particular case of resource-determined co-existence between two species. Essential to our definitions is the fact that co-occurrence may be affected by different resource requirement as well as direct interaction between the two species.

In a current debate on community ecology (e.g. Connell 1980, 1983, Roughgarden 1983, Harvey et al. 1983, Conner and Simberloff 1983, Simberloff 1982, 1983, Strong et al. 1984) the central difficulty under discus-

sion is the deduction of dynamics from distribution patterns. Our discussion relates to this debate in a general sense, but in the following we do not wish to add fuel to this debate, but to stress the differences between the two concepts of association and interaction.

Definitions of association and interaction

Following Berryman (1981), we may conceptualize how a species interacts with its environment as in Fig. V:1; the environment is composed of both abiotic and biotic components. We may separate out one of the species (B, say) constituting the environment for species A. Species A and B may, for example, utilize similar environmental resources (biotic as well as abiotic).

On the basis of current ecological thinking (e.g. May 1981) we suggest that association measures the similarity of two (or more) species' relations to their environment; this is denoted as α in Fig. V:2. Interaction measures, on the other hand, the species' mutual effects on each other's population dynamics [e.g. specific growth rate, $(1/x) \cdot dx/dt$ where x is the density of the species]; this is denoted as β in Fig. V:2. Thus defined, we believe that these concepts may be separated on the basis of data.

Association then, relates to habitat and resource preferences: Two species are highly associated whenever their maximal specific net rates of population increase are approximately equal under similar environmental conditions, and the degree of association is higher the more equal the net rates are. Looking at the problem of association this way, 'no association' is concluded to occur if the niches of two species do not overlap at all. Consequently, maximal association occurs when the niches overlap as much as they can, constrained by 'the limiting similarity' (see, e.g., Christiansen and Fenchel 1977, Roughgarden 1979).

Interactions, on the other hand, comprise the mutual influence (positive and negative) on each species' net specific population growth rate. Whenever the net effect of this influence is positive, it is called mutualism; otherwise it is called competition (see, e.g. Odum 1971). Obviously, asymmetric interactions may occur.

Competition as well as mutualism may be mediated through the environment. If so, we call it exploitative interaction; whereas if it is a direct interaction, we call it interference interaction. These terms

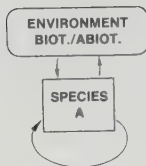


Figure V:1. A population of one species regulated by intraspecific as well as environmental parameters. The environment incorporates biotic and abiotic components.

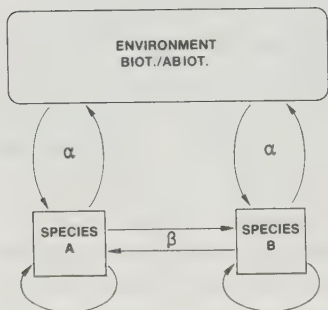


Figure V:2. Populations of two interacting species. The interaction (β) is the mutual influence of the two species, while their relation through the environment (α) is regarded as the association.

correspond to Nicholson's (1933, 1954) concept of exploitative (or scramble) and interference (or contest) competition.

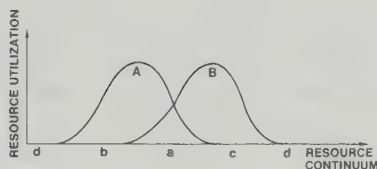
HOW ARE ASSOCIATION AND INTERACTION RELATED TO NICHE SPACING?

Assume a resource axis in a niche-theoretical sense (Hutchinson 1957). Let for example, the axis be humidity, temperature, or degree of exposure. That is, we consider, as also done by Hutchinson, the niche axis in a one-to-one relation to a spatial gradient. Then, two adjacent locations on this axis will be adjacent in space, too.

Now, assume that we take samples randomly along such an axis and count how many observations that fall into the four categories a, b, c, and d defined in Fig. V:3. The frequencies of these classes correspond directly to the quantities used in a 2×2 presence-absence table commonly employed for estimating how pairs of species relate to each other (e.g. Pielou 1977, Southwood 1978).

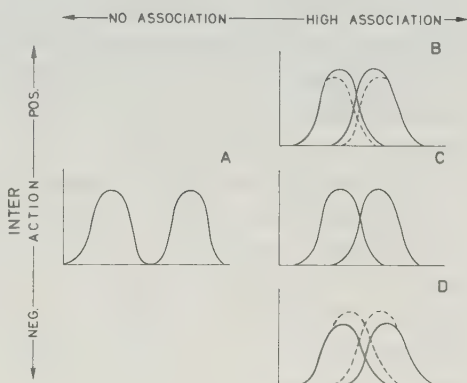
Figure V:3. The utilization by two species, A and B, of a resource distributed over a niche axis in a one-to-one relation to a spatial gradient.

a, b, c and d refer to the 2 x 2 contingency table.



	B	$\bar{B}$	
A	a	b	a+b
$\bar{A}$	c	d	c+d
	a+c	b+d	k=a+b+c+d

Figure V:4. Various types of coexistence of two species, illustrated as a one-dimensional niche. a) At zero or no association the species have non-overlapping niches. When the species are associated there is an overlap in their niches. The degree of overlap is dependent on the intensity of the interaction. b) At positive interaction the realized niches are larger in sympatry (solid lines) than in allopatry (dashed lines). c) When the interaction is neutral the realized niches are not affected. d) At negative interaction, realized niches are smaller in sympatry (solid lines) than in allopatry (dashed lines).



From Fig. V:4 we see that measuring interaction is not meaningful when there is no association between the considered species-pair. In cases with high association, we have that the utilization curves (as used by, e.g. Christiansen and Fenchel 1977) of the two species by definition are greatly overlapping. But as pointed out by several authors (e.g. Colwell and Futuyma 1971, Vandermeer 1972; see also Schoener 1983), only knowing that this overlap is great tells nothing about whether interaction is positive, neutral or negative. To settle which type of interaction applies, we must compare the realized niches of the two species when in allopatry and in sympatry. This is illustrated in Fig. V:4.

If we treat the relations between species this way (Figs V:3-4) it can be demonstrated that the physical size of the sampling unit becomes rather important. The larger it is, the more probable it is that a large portion of the niche axis is incorporated. Hence, we may estimate different degrees of association depending on the physical size of the sample. This makes comparison between index-values obtained on the basis of different studies difficult.

ON DEFINING THE NULL-CASE OF 'NO INTERACTION'

Engen (1985) discusses this rather thoroughly.

The essential effect of interaction (competition and mutualism) is that each species is affected by the other species through their net growth rates, $(1/x) \cdot dx/dt$. Following Engen (1985: $H_0^{(1)}$ -case) we may define the null-case (of no interaction) as: Let an island be inhabited by two species A and B. For each species x and y individuals are present, respectively; $x \geq 0$, $y \geq 0$. When there is no interspecific competition (nor mutualism) it is assumed, by definition, that the net growth rate only depends on x and y through their sum, $x + y$; i.e., the total density of individuals on the island. In this case individuals of each species ignore the fact that there are two species coexisting while the effect of total density is accounted for.

This seems a biologically reasonable definition. It is, however, not the only one. Others (see, e.g. Cole 1949, Morisita 1959, Hurlbert 1969, Ratliff 1982, Engen 1985: his $H_0^{(2)}$), have defined the null-case, implicit or explicit, as: Consider an island as above. The density dependent component of the net growth rates for species A or B are assumed to depend solely on x and y , respectively. This model implies that the two species are merely sharing the same space, and that they are not influencing each other (not even spatially!) in any other way. We believe that this is a too strong (and artificial) restriction of the definition of the null-case, since it does not compensate for total density.

METHODS FOR MEASURING ASSOCIATION AND INTERACTION

The arguments above seem to motivate the use of abundance data for measuring interaction. Unfortunately only a few methods applying such abundance data are available (see Boesch 1977 for review). Presence-absence data are unsuitable for the purpose of measuring interaction, because only the most pronounced cases of interactions would thus be detected.

Association, on the other hand, relates to the presence or absence of necessary resources. Then, species may be present or absent depending on which resources are available. Therefore, it seems reasonable (even though we cannot prove this) to measure association by presence-absence data even though abundance-data in this case may be appropriate. Several methods using such data are available (for reviews, see Southwood 1978, Janson and

Vegelius 1981). Notice, however, that there is no a priori reason for not assuming abundance data also to provide information on the degree to which two species are associated.

Employing a $(2 \times 2) \chi^2$ -method for measuring association could provide an objective criteria for separating negative association ($a < E_a$) from positive ($a > E_a$), where $E_a = [(a + b)(a + c)]/k$ (symbols according to Fig. V:3).

Our suggestion of applying abundance data for measuring interactions, and presence-absence or abundance data for measuring associations, is a further development of an idea originally presented by Hurlbert (1969: 5). he stated that 'ecologists who measure association with presence-absence data and ecologists who measure association with abundance data, clearly are not studying the same thing'. Similar ideas were presented by Colwell and Futuyma (1971).

A MODEL

The situation we have in mind may - as an example - be precisely expressed by a mathematical model. Consider a group of physically identical islands on which maximally two species - 1 and 2 - live.

Let λ_i ($i = 1, 2$) be the colonization rates for the two species onto these islands. On a set of islands exposed to the same source of colonizing species (both types and numbers), the difference between λ_1 and λ_2 measures, according to the argument presented in Section 2, the two species' association; the larger $|\lambda_1 - \lambda_2|$ [or some unit-less quantity like $|\lambda_1 - \lambda_2| / (\lambda_1 + \lambda_2)$] is, the weaker is the association between the two species. The interaction between the two species is, further, measured by a density dependence parameter, b . Negative interaction occurs whenever $b > 1$; positive or mutualistic interaction occurs whenever $b < 1$; $b = 1$ represents the neutral case of no interaction. Utilizing these definitions, an appropriate model for the population dynamics of the two species (whose abundances are given by x and y) are

$$\frac{dx}{dt} = \lambda_1 - c \cdot x(x + b \cdot y) \quad (V:1)$$

$$\frac{dy}{dt} = \lambda_2 - c \cdot y(y + b \cdot x)$$

where c is some positive scaling factor. Notice that we, in order to simplify, have assumed a symmetric type of interaction. Obviously, we obtain the more general case when substituting b by $b_1 \neq b_2$; however, since this only will add to the complexity without providing any new insight, we will not treat the asymmetric case of $b_1 \neq b_2$.

Model (1) corresponds to a dynamically stable situation with damped oscillations; see Fig.V:5. For $b = 1$ it will represent a null-case as defined by Engen [1985: his Example 2 in Section 3 corresponding directly to model(V:1) above]. We have generated data for testing our idea of how to detect association and interaction, utilizing a stochastic model similar to the deterministic model(V:1). Each simulation was started at equilibrium and ran for about 25 iterations. Two versions of the stochastic model have been analyzed:

(i) In one version, only one of the species changes its abundance at any time; furthermore, when the density of a species changes, only one individual is added or subtracted.

(ii) The other version was constructed in order to make the generated data material resemble a more realistic island biogeographic situation, which was the type of real data that we also use in this paper. In this latter version, the colonization parameter λ was drawn from a normal distribution with mean value λ . Further, when one of the species was 'found' by the stochastic simulation to increase its abundance, this was done by adding a number of individuals drawn from a Poisson distribution with parameter μ (estimated by $\bar{x}$). In this case, x and y are, in the simulations, found to result in an approximate negative binomial distribution of x and y (a distribution commonly found in parasitological materials; Davids 1973, Randolf 1975, Anderson and May 1978, Nilsson and Lundqvist 1978). When one of the species was 'found' by the stochastic simulation to decrease its abundance, this was done by subtracting one individual at a time.

TEST STATISTICS

To investigate the validity of our ideas expressed in Sect. 4, two indices have been used, one based on presence-absence data and another based on

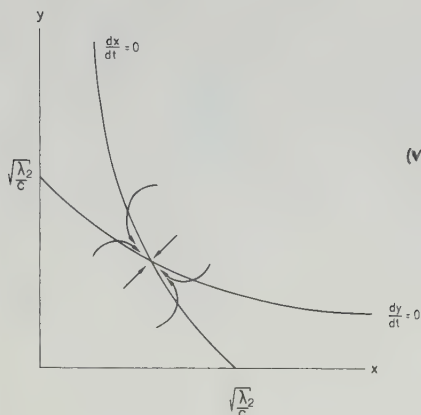


Figure V:5. Analysis of ecological stability in model (V:1). Since the x-isocline ($dx/dt=0$) and the y-isocline ($dy/dt=0$) always intersect as depicted in this phase-diagram, model (V:1) will always give rise to a dynamically stable equilibrium. See the main text for definitions of symbols.

abundance data. In addition to the simulated data-set generated by the model described in Sect. 6 we have also used real data derived from a study on ectoparasites on small rodents carried out by the parasitological laboratory at the Department of Animal Ecology, University of Lund.

As the presence-absence statistics, we employ the χ^2 -statistics recommended by Southwood (1978). Its sample estimate is defined as

$$\chi^2 = k \cdot \left[|a \cdot d - b \cdot c| - (k/2) \right] 2 / \left[(a+c) \cdot (b+d) \cdot (a+b) \cdot (c+d) \right] \quad (V:2)$$

where the various quantities entering this formula are defined in Fig. V:3. The critical 5%-level with 1 degree of freedom for this test is 3.84; i.e., two species are positively or negatively associated if $\chi^2_{[1]} > 3.84$.

As the abundance statistics, we apply Morisita's (1959) covariation statistics - a variant of the standard covariance statistics. Its sample estimate is defined by

$$R = \begin{cases} R' & \text{if } R' \geq 0 \\ [(k \cdot \sum_{i=1}^k x_i \cdot y_i) / (N_x \cdot N_y)] - 1 & \text{otherwise} \end{cases} \quad (V:3)$$

where

$$N_x = \sum_{i=1}^k x_i \quad \& \quad N_y = \sum_{i=1}^k y_i$$

and

$$R' = 2 \cdot (k \sum_{i=1}^k x_i \cdot y_i - N_x \cdot N_y) / (k \cdot (\delta_x + \delta_y) \cdot N_x \cdot N_y)$$

where further

$$\delta_x = \left[\sum_{i=1}^k x_i (x_i - 1) \right] / [N_x \cdot (N_x - 1)]$$

and

$$\delta_y = \left[\sum_{i=1}^k y_i (y_i - 1) \right] / [N_y \cdot (N_y - 1)]$$

Both indices [i.e. (V:2) and (V:3)] are commonly used in the ecological literature (e.g. Southwood 1978).

RESULTS AND DISCUSSION

In summary we expect the χ^2 -test, based on presence-absence data, to be sensitive to changes in $|\lambda_1 - \lambda_2|$; high values of $|\lambda_1 - \lambda_2|$ (low association) should give low χ^2 -values. The χ^2 statistics are further expected to be high if b is high ($b > 1$) (i.e. negative interaction) and low if b is small ($b < 1$) (i.e. positive interaction). Furthermore, we expected Morisita's R-index, based on abundance (or frequency) data, to be sensitive to changes in b and - to a lesser degree - on changes in $|\lambda_1 - \lambda_2|$; small values of b ($b < 1$ (positive interaction)) should give high R-values and large values of b ($b > 1$ (negative interaction)) should give low R-values - and high values of $|\lambda_1 - \lambda_2|$ (low association) should give low R-values. Since we define our null-case of no interaction differently from Morisita (1959), we would not expect Morisita's index to take on positive values in our simulation model.

Simulated Data

Morisita's index is sensitive to changes in interaction (Tabs V:1-2). There is a high positive correlation (0.9) between R and $\log(b)$ (Fig. V:6 A & B - top diagrams); the log-transformation has been used for convenience and in order to obtain as good a correlation as possible. This means that about 80 % of the variation in the R value can be explained by the variation in b . The correlation between R and association $|\lambda_1 - \lambda_2|$ (Fig. V:6 A & B - middle diagrams) is small (0.2 - 0.3) and explains only 5 - 10 % of the variation in R . Consequently, Morisita's R-index seems to be rather insensitive to association, and, therefore, a good tool to measure interaction as defined in our model.

The correlation between association and the χ^2 -value is low (Fig. V:6 C & D - middle diagrams), and explains only 15 - 25 % of the variation in the χ^2 -value. There is a somewhat higher correlation between χ^2 and $\log(b)$ (Fig. V:6 C & D - top diagrams), which explains about 30 % of the variation in the χ^2 . A combination between association and interaction, expressed as $[\log(b) - |\lambda_1 - \lambda_2|]$ (Fig. V:6 C & D - bottom diagrams), gives a correlation coefficient of 0.7 which explains about 50 % of the variation in the χ^2 -value.

Figure V:7 summarizes our theoretical conclusions: A high R value (that is only slightly negative), indicates positive interaction and together with a low to intermediate χ^2 -value the association is low to high. A

Table V:1. Statistical tests applied on simulated data. The model is described in the text [version (i)]. In the table, λ is a constant and at population increase one individual is added. $\lambda_A = 1$.

		Positive interaction		Neutral		Negative interaction	
		0.01	0.1	1.0	10.0	100.0	1000.0
b							
λ_B/λ_A							
High association	1	R: -0.183	R: -0.129	R: -0.249	R: -0.547	R: -0.573	R: -0.599
		χ^2 : 0.251	χ^2 : 0.057	χ^2 : 1.408	χ^2 : 9.979	χ^2 : 5.540	χ^2 : 6.336
	2	R: -0.092	R: -0.124	R: -0.247	R: -0.393	R: -0.548	R: -0.529
		χ^2 : 0.205	χ^2 : 0.000	χ^2 : 0.234	χ^2 : 3.567	χ^2 : 2.667	χ^2 : 2.879
	3	R: -0.030	R: -0.023	R: -0.129	R: -0.379	R: -0.496	R: -0.466
		χ^2 : 0.031	χ^2 : 0.457	χ^2 : 0.362	χ^2 : 1.547	χ^2 : 1.836	χ^2 : 0.691
Low association	4	R: -0.012	R: -0.018	R: -0.072	R: -0.366	R: -0.466	R: -0.498
		χ^2 : 0.007	χ^2 : 0.077	χ^2 : 0.000	χ^2 : 2.291	χ^2 : 2.420	χ^2 : 2.698

Table V:2. Statistical tests applied on simulated data. The model is described in the text [version (ii)]. In the table, λ is drawn from a normal distribution with mean value λ and the variance $\lambda/100$. At population increase a number of individuals, drawn from a Poisson distribution with parameter μ , was added. $\lambda_A = 1$.

		Positive interaction			Neutral			Negative interaction		
		b								
		λ_B/λ_A								
		0.01			0.1			1.0		
		100.0			10.0			100.0		
		1000.0								
High association	1	R: -0.143	R: -0.210	R: -0.248	R: -0.509	R: -0.667	R: -0.590			
		χ^2 : 0.023	χ^2 : 0.059	χ^2 : 1.665	χ^2 : 13.189	χ^2 : 12.544	χ^2 : 7.176			
	2	R: -0.040	R: -0.124	R: -0.286	R: -0.494	R: -0.538	R: -0.554			
		χ^2 : 0.446	χ^2 : 1.779	χ^2 : 4.199	χ^2 : 11.194	χ^2 : 6.167	χ^2 : 6.167			
Low association	3	R: -0.146	R: -0.201	R: -0.150	R: -0.399	R: -0.498	R: -0.482			
		χ^2 : 0.034	χ^2 : 0.024	χ^2 : 3.953	χ^2 : 5.482	χ^2 : 3.200	χ^2 : 3.368			
	4	R: -0.080	R: -0.115	R: -0.245	R: -0.353	R: -0.460	R: -0.507			
		χ^2 : 0.530	χ^2 : 0.412	χ^2 : 0.704	χ^2 : 0.020	χ^2 : 0.007	χ^2 : 3.176			

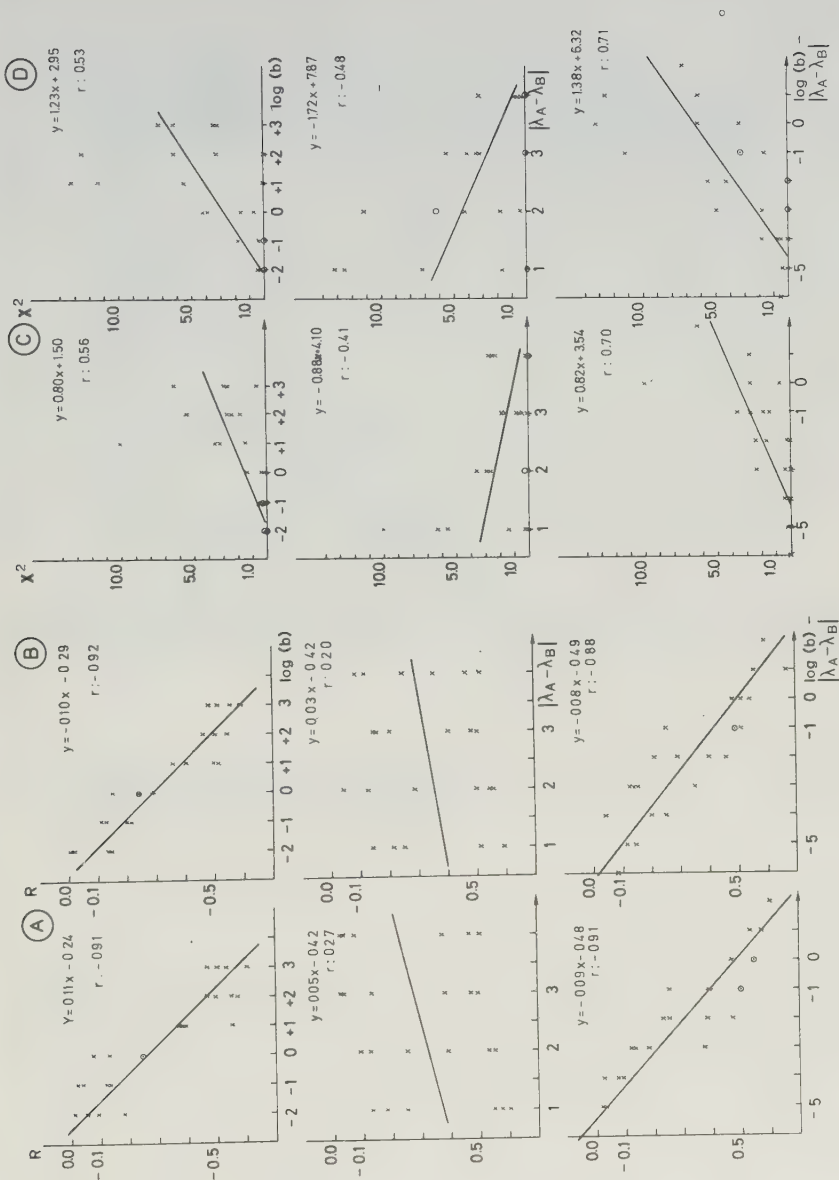
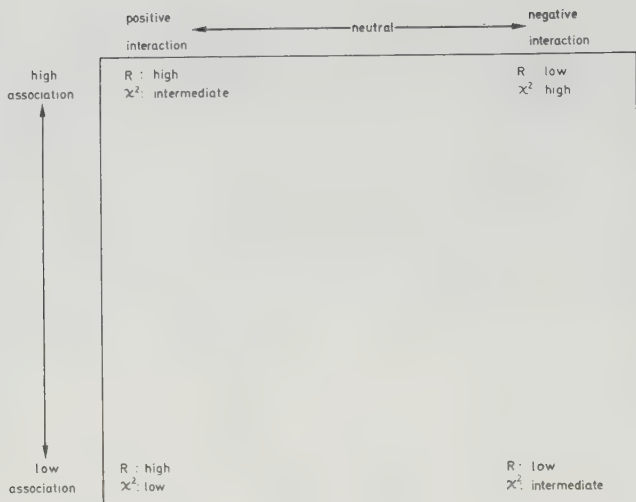


Figure V:6. Linear regression analysis of association ($\lambda_A - \lambda_B$) and interaction (b) versus Morisita's index (R) and X^2 (Southwood 1978). Linear regression is shown for R and X^2 against $\log(b)$, $\lambda_A - \lambda_B$, and interaction and association combined into $\log(b) - |\lambda_A - \lambda_B|$, respectively. A and C are based on results from our simulation model, version (i) (see Tab. V:1), and B and D are based on results from our simulation model, version (ii) (Table V:2).



Figur V:7. Expected behaviour of Morisita's R-index and the χ^2 -value (Southwood 1978), as found in the simulated material. See the main text for details.

low R value indicates negative interaction, and the χ^2 -value can be expected to range between intermediate and high, indicating negative or positive association.

Real-life Data

Our simulation model, version (i), corresponds to a density dependent population growth; as defined it is an equilibrium model. This is probably not a very likely situation to occur in nature; but this version is easy to visualize as a mathematical model - it represents a reference point.

In our model-version (ii) the island population changes through step-wise density increments or decrements. This corresponds to, for example, an ectoparasitic species invading its host in batches like ticks, most fleas and several mesostigmatic mites. These ectoparasites are encountered by the host when moving in the terrain. The parasites are restricted to certain places, like nests and run-ways. Under such circumstances it is likely that more than one individual invade the host at the same time (paper I).

Table V:3. Statistical tests applied on a real data set of ectoparasites from the wood mouse *Apodemus sylvaticus*. n = number of parasites. N = number of hosts infested by the parasite species, J = number of joint occurrences, R = Morisita's index.

Ixodes		Species						
ricinus		n/N						
358/46		J R X²						
15	Eulaelaps							
0.0	stabularis							
0.005	49/16							
3	1	Haemogamasus						
-0.679	-0.480	nidi						
0.170	0.320	4/3						
37	13	2	Laelaps					
0.0	0.0	-0.605	agilis					
0.233	0.001	0.045	226/40					
15	8	2	13					
0.0	0.0	0.0	-0.043					
0.028	1.934	0.398	0.014					
			Ctenophthalmus					
			agyrtes					
			29/17					
18	7	2	17	8				
0.0	0.0	0.0	0.0	0.0				
0.125	0.113	0.222	1.266	0.514				
				Typhloceras				
				poppei				
				33/19				
8	5	1	7	4	5			
0.0	0.0	-0.019	0.0	0.0	0.0			
0.223	1.761	0.002	0.155	0.152	0.759			
					Nosopsyllus			
					fasciatus			
					13/9			
3	2	0	3	0	1	0		
0.0	0.0	-1.0	0.0	-1.0	-0.485	-1.0		
0.170	0.514	0.670	0.045	0.398	0.221	0.002		
						Rhadinopsylla		
						pentacantha		
						3/3		
3	2	0	2	2	0	0		
-0.430	0.0	-1.0	-0.549	0.0	0.0	-1.0		
0.170	0.514	0.670	0.045	0.398	0.221	0.002		
						Hoplopleura		
						acanthopus		
						3/3		
13	6	0	13	6	6	4	1	1
-0.236	0.0	-1.0	0.0	-0.121	-0.438	0.0	0.0	-0.327
0.895	0.098	0.320	0.001	0.011	0.083	0.287	0.320	0.320
								Polyplax
								spinulosa
								22/16

Morisita's index is never found to be positive for this data set. In three cases it is less than -0.5, in all with low to moderate X^2 values. In no case is the X^2 -value (significantly) high. Three times it is more than 1.0, all with R equal zero (but see also paper III). This suggests a system dominated by low association and negative interaction between the considered ectoparasites. (Tab. V:3).

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References

- Abbott, I. 1983. The meaning of z in species/area regressions and the study of species turnover in island biogeography. - *Oikos* 41: 385-390.
- Anderson, R.M. 1976. Dynamic aspects of parasite population ecology. - In: C.R. Kennedy (ed.). Ecological aspects of parasitology. North-Holland publishing Company. Amsterdam.
- Anderson, R.M. and R.M. May. 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. - *J. Anim. Ecol.* 47: 219-249.
- Andersson, Å. and L. Hansson, 1966. Småäggdjursundersökningar i norra Norge 1965. - *Fauna och Flora* 61: 49-72.
- Arthur, D.R. 1962. Ticks and disease. - Pergamon Press. London.
- Artz, V. 1975. Zur Synökologie der Ektoparasiten von Kleinsäugetern in Norddeutschland. (Siphonaptera, Phthiraptera, Acarina, Coleoptera: Leptinidae). - *Ent. Germ.* 1: 105-143.
- Berryman, A.A. 1981. Population systems. A general introduction. - Plenum Press, New York.
- Bliss, C.I. and R.A. Fischer. 1953. Fitting the negative binomial distribution to biological data. - *Biometrics* 9: 176-200.
- Boesch, D.F. 1977. Application of numerical classification in ecological investigations of water pollution. - *Ecol. Res. Series*, EPA-600/3-77-033.
- Brinck, G. 1966. Siphonaptera from small mammals in natural foci of tick-borne encephalitis virus in Sweden. - *Opusc. Ent.* 31: 156-170.
- Brinck-Lindroth, G. 1972. Subspecific differentiation and distribution of the flea Palaeopsylla soricis (Dale) and Malareus penicillig penicilliger (Grube) in Fennoscandia. - *Ent. scand.* 3: 297-312.
- Brinck-Lindroth, G., L. Lundqvist and A. Nilsson. 1984. Control of the human head louse with disulfiram and bezyl benzoate emulsions. - *Acta Derm. Venereol.* (Stockholm). 64: 325-330.
- Camin, J.H. 1964. Application of behavioral data to problems of laboratory rearing of parasitic acarines. - *Acarologia*, fasc. h.s. (C.R.I. Congrès Int. d'Acarologie 1963). 350-356.
- Christiansen, F.B. and T.M. Fenchel. 1977. Theories of populations. - Springer Verlag, Berlin.
- Cole, L.C. 1949. The measurement of interspecific association. - *Ecology* 30: 411-424.
- Colwell, R.K. and D.J. Futuyma. 1971. On the measurement of niche breadth and overlaps. - *Ecology* 52: 567-576.
- Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. - *Oikos* 35: 131-138.
- 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. - *Am. Nat.* 122: 661-696.
- Conner, E.F. and D. Simberloff. 1983. Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. - *Oikos* 41: 455-465.
- Crofton, H.D. 1971. A quantitative approach to parasitism. - *Parasitology* 62: 179-193.
- Daniel, M. and B. Holubičková. 1972. Interspecific relationships of gamasoid mites in the nests of Clethrionomys glareolus. - *Folia Parasit.* 19: 67-86.
- Darskaya, N.F. and L.G. Suvorova. 1984. The flea fauna of the tick-borne encephalitis focal region in the eastern part of the Russian plain. - *Folia Parasit.* 31: 69-77.
- Davids, C. 1973. The water mite Hydrachna conjuncta Koenike, 1895, biodynamics and relation to species of Corixidae. - *Neth. J. Zool.* 23: 363-429.

- Dritschilo, W., H. Cornell, D. Nafus, and B. O'Conner. 1975. Insular biogeography: Of mice and mites. - Science 190: 467-469.
- Edler, A. 1972. Ectoparasitic mites (Acarina) from small mammals in Central Sweden. - Ent. Tidskr. 90: 272-284.
- 1973. Seasonal changes and host relationships of mites on small mammals in southern Sweden. - Folia Parasit. 20: 75-87.
- Edler, A. and R. Mehl. 1972. Mites (Acari, Gamasina) from small mammals in Norway. - Norsk ent. Tidsskr. 19: 133-147.
- Edler, A. and M. Mrčiak. 1975. Gamasina mites (Acari: Parasitiformes) on small mammals in northernmost Fennoscandia. - Ent. Tidskr. 96: 167-177.
- Edler, A. and L. Solomon. 1979. Morphology of preadult stages of Laelaps agilis Koch, 1836 with notes on life history and feeding habits (Acari/ Mesostigmata: Laelapidae). - Ent. scand. 10: 81-90.
- Engen, S. 1985. Association between pairs of species. The association between pairs of species on discrete habitat units. - Biometrics 40: 729-738.
- Erlinge, S., G. Göransson, L. Hansson, G. Högstedt, O. Liberg, I.N. Nilsson, T. Nilsson, T. von Schantz and M. Sylven. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. - Oikos 40: 36-52.
- George, R.S. and G.B. Corbet, 1959. A collection of fleas (Siphonaptera) from small mammals in the Scottish highlands. - Entom. Gaz. 10: 147-158.
- Gliwicz, J. 1983. Survival and life span. In: K. Petrusiewicz, (ed.). Ecology of the bank vole. - Acta theriol. Suppl. 1: 161-172.
- Haitlinger, R. 1983. Arthropod communities. In: K. Petrusiewicz (ed.). Ecology of the bank vole. - Acta theriol. Suppl. 1: 55-68.
- Halvorsen, O. 1976. Negative interaction amongst parasites. - In: C.R. Kennedy (ed.). Ecological aspects of parasitology. North Holland publishing company. Amsterdam, Oxford.
- Hämet-Ahti, L. 1963. Zonation of mountain birch forest in northernmost Fennoscandia. - Ann. Bot. Soc. Vanamo 34: 1-127.
- Hansson, L. 1971. Smågnagare - deras betydelse, föda, beståndsvariationer och regulation. - Sveriges Natur Årsbok. - 1981. Viltekologi. Signum. Lund.
- Hansson, L., J. Löfqvist and A. Nilsson. 1978. Population fluctuations in insectivores and small rodents in northernmost Fennoscandia. - Z. f. Säugetierkunde 43: 75-92.
- Harvey, P.H., R.W. Colwell, J.G. Silvertown and R.M. May. 1983. Null models in ecology. - Ann. Rev. Ecol. Syst. 14: 189-212.
- Hurlbert, S.H. 1969. A coefficient of interspecific association. - Ecology 50: 1-9.
- Hutchinson, G.E. 1957. A treatise on limnology. (Vol. 1): Geography, physics and chemistry. - Wiley, New York.
- Janion, S.M. 1983. Dynamics of an ectoparasite host system. In: K. Petrusiewicz (ed.). Ecology of the bank vole. - Acta theriol. Suppl. 1: 69-73.
- Janson, S. and J. Vegelius. 1981. Measures of ecological association. - Decologia 49: 371-376.
- Kennedy, C.R. 1975. Ecological animal parasitology. - Blackwell Scientific Publications. Oxford, London, Edinburgh, Melbourne.
- Levins, R. 1968. Evolution in changing environments. - Princeton University Press. Princeton.
- Lundqvist, L. 1974. Gamasina mites (Acari, Parasitiformes) from nests of the mole Talpa europaea L. - Ent. scand. 5: 39-48.
- MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. - Princeton University Press. Princeton.

- Marshall, A.G. 1981. The ecology of ectoparasitic insects. - Academic Press. London, New York, Toronto, Sydney, San Francisco.
- May, R.M. (ed.). 1981. Theoretical ecology. - Blackwell Scient. Publ. Oxford.
- Mazurkiewicz, M. 1983. Spatial organization of the population. In: K. Petrusiewicz (ed.). Ecology of the bank vole. - Acta theriol. Suppl. 1: 117-128.
- Mazurkiewicz, M. 1983 Spatial organisation of the population. In: K. Petrusiewicz (ed.). Ecology of the bank vole. - Acta theriol. Suppl. 1: 117-127.
- Michielsen, N.C. 1966. Intraspecific and interspecific competition in the shrews Sorex araneus L. and S. minutus L. - Archives Néerlandaises de Zoologie 17: 73-174.
- Mohr, C.O. 1961. Relation of ectoparasite load to host size and standard range. - J. Parasitol. 47: 978-984.
- Mohr, C.O. and W.A. Stumpf. 1964. Louse and chigger infestations as related to host size and home ranges of small mammals. - Trans. 29th. N. Am. Wildl. nat. Res. Conf.: 181-195.
- Morisita, M. 1959. Measuring of interspecific association and similarity between communities. - Mem. Fac. Sci. Kyushu Univ., Ser. E. (Biol.) 3: 65-80.
- Mrciak, M., M. Daniel and B. Rosický. 1966. Parasites and nest inhabitants of small mammals in the western Carpathians. I. Mites of the superfamily Gamasoidea (Parasitiformes). - Acta F.R.N. Univ. Comen. 12. - Zoologia, 13: 81-116.
- Myllymäki, A. 1977. Intraspecific competition and home range dynamics in the field vole Microtus agrestis. - Oikos 29: 553-569.
- Nelson, W.A. 1984. Effects of nutrition of animals on their ectoparasites. - J. Med. Ent. 21: 621-635.
- Nicholson, A.J. 1933. The balance of animal populations. - J. Anim. Ecol. 2: 132-178.
- 1954. An outline of the dynamics of animal populations. - Aust. J. Zool. 2: 9-65.
- Nilsson, A. 1974a. Distribution, host relations and seasonal occurrence of Ixodes trianguliceps Birula (Acari) in Fennoscandia. - Folia Parasit. 21: 233-241.
- 1974b. Host relations and population changes of Ixodes trianguliceps (Acari) in northern Scandinavia. - Oikos 25: 315-320.
- 1978. Ticks and their small mammal hosts. A study on dynamics and host relations of Ixodes ricinus and I. trianguliceps. Dissertation. University of Lund.
- 1981. Spatial differentiation of ectoparasites on small mammals. - Holarctic ecology 4: 184-190.
- Nilsson, A. and L. Lundqvist. 1978. Host selection and movements of Ixodes ricinus (Acari) larvae on small mammals. - Oikos 31: 313-322.
- Nutall, G.H.E. 1917. The biology of Pediculus humanus. - Parasitology 10: 80-185.
- Odum, E.P. 1971. Fundamentals of ecology. - Saunders, Philadelphia.
- Osbrink, W.L.A. and M.K. Rust, 1984. Fecundity and longevity of the adult cat flea, Ctenocephalides felis felis (Siphonaptera: Publicidae). - J. Med. Entomol. 21: 727-731.
- Peus, F. 1972. Zur Kenntnis der Flöhe Deutschlands. IV. Faunistik und Ökologie der Säugetierflöhe. - Zool. Jb. Syst. 99: 408-504.
- Pielou, E.C. 1977. An introduction to mathematical ecology. - Wiley-Intersciences. New York.
- Price, P.W. 1980. Evolutionary biology of parasites. - Princeton University Press. Princeton.
- Randolph, S.E. 1975. Patterns of distribution of the tick Ixodes trianguliceps Birula on its hosts. - J. Anim. Ecol. 44: 451-474.

- Ratliff, D.R. 1982. A correction of Cole's C_7 and Hurlbert's C_8 coefficients of interspecific association. - Ecology 63: 1605-1606.
- Rechav, Y., R.A.I. Norval, J. Tannock and J. Colborne. 1978. Attraction of the tick Ixodes neitzi to twigs marked by the klipspringer antelope. - Nature 275: 310-311.
- Robbins, R.G. and G.D. Faulkenberry. 1982. A population model for fleas of the gray-tailed vole, Microtus canicaudus Miller. - Ent. News. 93: 70-74.
- Rothschild, M. and R. Ford. 1964. Breeding of the rabbit flea [Spilopsyllus cuniculi (Dale)] controlled by the reproductive hormones of the host. - Nature 201: 103-104.
- Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. - MacMillan, New York.
- 1983. Competition and theory in community ecology. - Am. Nat. 122: 583-601.
- Schoener, T.W. 1983. Field experiments on interspecific competition. - Am. Nat. 122: 240-285.
- Simberloff, D. 1976. Species turnover and equilibrium island biogeography. - Science 194: 572-578.
- 1982. The status of competition theory in ecology. - Ann. Zool. Fennici 19: 241-253.
- 1983. Competition theory, hypothesis - testing, and other community ecological buzzwords. - Am. Nat. 122: 626-635.
- Sokal, R.R. and F.J. Rohlf. 1969. Biometry. - W.H. Freeman and company. San Francisco.
- Sonenshine, D.E. and J. Stout, 1968. Tick burdens in relation to spacing and range of hosts in Dermacentor variabilis. - J. Med. Ent. 5: 49-52.
- Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? - J. Anim. Ecol. 46: 337-365.
- 1978. Ecological methods. - Chapman & Hall. London.
- Stenseth, N.C. 1983. Causes and consequences of dispersal in small mammals. - In: I.R. Swingland, and P.J. Greenwood (eds). The ecology of animal movement. Clarendon Press/Oxford Univ. Press. Oxford.
- Strong, D.R., Jr, D. Simberloff, L.G. Abele and A.B. Thistle (eds). 1984. Ecological communities. Conceptual issues and the evidence. - Princeton Univ. Press, Princeton.
- Tenerio, J.M. and F.J. Radowsky, 1979. Review of the subfamily Hirstionysinae, synonymy of Echinonyssus Hirst and Hirstionyssus Fonseca, and description of four new species of Echinonyssus (Acari: Laelapidae). - J. Med. Entomol. 16: 370-412.
- Uchikawa, K. 1967. An ecological study on the fleas in the Yatsugatake range. (I) On the fleas found on the small mammals trapped in the subalpine forest. - Jap. J. Ecol. 17: 43-49.
- Ulmánen, I. and A. Myllymäki. 1971. Species composition and numbers of fleas (Siphonaptera) in a local population of the field vole, Microtus agrestis (L.). - Ann. Zool. Fennici 8: 374-384.
- Wakelin, D. 1976. Host responses. - In: C.R. Kennedy, (ed.). Ecological aspects of parasitology. North-Holland publishing company. Amsterdam.
- Vandermeer, J.H. 1972. Niche theory. - Ann. Rev. Ecol. Syst. 3: 107-132.

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